INFLUENCE OF MOISTURE ON DENSITY AND DISTRIBUTION OF GRASSLAND BIRDS IN NORTH DAKOTA

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Abstract. High annual variation in grassland bird populations in the Great Plains has often been attributed to changes in moisture levels, but most previous assessments of variation in grassland bird numbers have been of short duration, have occurred during a limited range of moisture levels, have been limited in geographic scope, have considered few species, or have sampled only one or few habitat types. Data from the long-term North American Breeding Bird Survey have the potential to overcome some of these shortcomings. We used linear models and information-theoretic methods to examine associations between moisture levels and populations of 17 species of grassland passerine and two species of wetland passerine in northern North Dakota from 1980 to 2004. We used data from 13 Breeding Bird Survey routes to provide indices of bird abundance and regional dispersion; we used numbers of ponds containing water identified on annual May waterfowl surveys and the Palmer Drought Severity Index (PDSI) as regional moisture indices. Responses varied among species, but the data indicated substantial support for moisture influencing the abundance of 17 of the 19 species we considered. Models including same-year pond numbers generally received more support than models including PDSI data. Dispersion of seven species throughout the study area was influenced by moisture levels, although the response was not as universal and support was not as strong as it was with abundance. Associations between grassland birds and moisture levels suggest the value of regional moisture indices to interpreting studies and surveys of grassland birds in the northern Great Plains.

Key words: climate, grassland birds, moisture, North American Breeding Bird Survey, population dynamics, Prairie Pothole region, precipitation.

Influencia de la Humedad sobre la Densidad y Distribución de Aves de Pastizal en Dakota del Norte

Resumen. La alta variación anual de las poblaciones de aves de pastizal en las Grandes Planicies ha sido frecuentemente atribuida a cambios en los niveles de humedad. Sin embargo, la mayoría de los estudios sobre las variaciones en los números de aves de pastizal han sido de corta duración, se han realizado durante periodos con una variación limitada de niveles de humedad, han sido limitados con respecto el área geográfica que abarcan, han considerado pocas especies o se han basado en muestreos realizados en uno o pocos tipos de hábitat. Los datos de largo plazo provenientes del Conteo de Aves Reproductivas de Norteamérica tienen el potencial de superar algunos de estos problemas. Utilizamos modelos lineales y métodos basados en la teoría de la información para examinar las asociaciones entre los niveles de humedad y las poblaciones de 17 especies de aves paseriformes de pastizal y dos especies de paseriformes de humedal en el norte de Dakota del Norte, desde 1980 a 2004. Utilizamos los datos de 13 rutas del Conteo de Aves Reproductivas para calcular índices de abundancia de aves y dispersión regional; utilizamos el número de charcas que contenían agua durante el conteo anual de aves de humedales realizado en mayo y el Índice de Severidad de Sequía de Palmer (ISSP) como un índice regional de humedad. Las respuestas variaron entre especies, pero los datos indicaron un apoyo substancial a la influencia de la humedad sobre la abundancia de 17 de las 19 especies que consideramos. Los modelos que incluyeron el número de charcas en el mismo año fueron generalmente mejor apoyados que los modelos que incluyeron los datos del índice ISSP. La dispersión de 7 especies en el área de estudio fue influenciada por los niveles de humedad, a pesar de que la respuesta no fue tan universal y que el soporte de los modelos no fue tan fuerte como para la abundancia. Las asociaciones entre las aves de pastizal y los niveles de humedad sugieren un valor en la utilización de los índices regionales de humedad para interpretar los estudios y muestreos de aves de pastizal en el norte de las Grandes Planicies.

INTRODUCTION

The Great Plains of North America are characterized by high annual and regional variation in precipitation (Wiens 1974, Bragg 1995, Woodhouse and Overpeck 1998). In the Prairie Pothole region of the northern Great Plains, variation in precipitation greatly influences soil moisture and the number of wetland basins containing water each year. High variation in bird abundance and distribution in response to changing wetland numbers and condition has been documented for waterfowl (Smith 1970, Stewart and Kantrud 1973, Brewster et al. 1976, Johnson and Grier 1988) and other waterbirds (Alisauskas and Arnold 1994, Peterjohn and Sauer 1997, Niemuth and Solberg 2003).

Associations between grassland bird abundance and seasonal moisture in the Great Plains are poorly understood, although many studies report substantial annual variation in numbers of grassland birds in response to moisture levels or precipitation. Wiens (1974) reported that the density of Horned Larks (*Eremophila alpestris*) in eastern Colorado was higher during a drought year than a year with higher precipitation, whereas densities of Western Meadowlarks (*Sturnella neglecta*), Lark Buntings (*Calamospiza melanocorys*), and Grasshopper Sparrows (*Ammodramus savannarum*) decreased. George et al. (1992) found that densities of Horned Larks, Sprague's Pipits (*Anthus spragueii*), Vesper Sparrows (*Pooecetes gramineus*), Grasshopper Sparrows, Clay-colored Sparrows (*Spizella pallida*), and Field Sparrows (*Spizella pusilla*) decreased between 1987 and 1988 during a severe drought in western North Dakota. Cody (1985), however, found that associations between grassland birds and precipitation in North Dakota varied among species and the period for which precipitation was recorded. Igl and Johnson (1999) reported that densities of Le Conte's Sparrows (*Ammodramus leconteii*) in Conservation Reserve Program (CRP) fields were positively correlated with precipitation over a seven-year period (1990–1996) in four states in the northern Great Plains. During this study, densities of Northern Harriers (*Circus cyaneus*), Sedge Wrens (*Cistothorus platensis*), Savannah Sparrows (*Passerculus sandwichensis*), and Le Conte's Sparrows were lower during a drought in 1990–1991 than during a wet period in 1995–1996; conversely, densities of Horned Larks, Chestnut-collared Longspurs (*Calcarius ornatus*), and Lark Buntings were lower during the wet years of 1995–1996 (Johnson 2005). Several mechanisms explaining precipitation-related fluctuations in abundance have been proposed, including changes in vegetation structure and composition, response to recent weather, variation in recruitment and productivity, and changes in food supplies (Wiens 1974, Cody 1985, Wiens 1989, George et al. 1992, Igl and Johnson 1999). Changes in abundance may not be immediate, due to philopatry, a lag in population growth, or delayed response by primary (e.g., vegetation) or secondary (e.g., invertebrates) resources used by birds.

The aforementioned observations were incidental to field studies that were of relatively short duration or occurred during a limited range of moisture levels. Also, most of the studies were limited in geographic extent or sampled only one or few habitat types, which affects inferences that can be made regarding responses of bird populations regionally to variation in precipitation. In contrast, the North American Breeding Bird Survey (BBS) is a long-term survey that covers most of North America and samples a wide variety of habitat types, but the influence of precipitation on grassland bird numbers as evidenced in BBS data is largely unknown. Increased understanding of regional population fluctuations is crucial to interpreting the biological significance of BBS trend estimates for some species of grassland birds (Peterjohn and Sauer 1999). An understanding of factors influencing population trends of grassland birds in the Great Plains may be particularly important, as grassland bird species richness is greatest in this region, especially in the northern Great Plains (Peterjohn and Sauer 1999), and grassland birds have a larger proportion of species that are decreasing than any other bird group in North America (Askins 1993, Peterjohn and Sauer 1999).

We used linear models and information-theoretic methods (Burnham and Anderson 1998) to evaluate associations between birds and moisture levels over a 25-year period in northern North Dakota. First, we assessed the weight of evidence for associations between grassland birds and same-year moisture levels as represented by the number of ponds containing water (collected by the U.S. Fish and Wildlife Service during May and referred to as May ponds) and the Palmer Drought Severity Index (PDSI; Palmer 1965). This enabled us to determine whether grassland bird data from the BBS revealed responses to precipitation similar to those identified by intensive local studies, as well as to determine which moisture index better explained variation in bird numbers. Second, we determined if support for associations between birds and moisture increased when indices from the year prior to bird sampling were included in models. This provided insight into whether birds were responding to moisture levels at the time of settling or cues such as condition of residual vegetation that were likely influenced by the previous year's moisture levels (i.e., a lag effect). Our analyses address some of the limitations of previous observations of grassland bird response to moisture because of the large geographic sampling frame, number of species assessed, multiple responses considered, and length of time considered. As BBS routes in the region are representative of the composition of upland land-cover classes in the surrounding landscape (Niemuth et al. 2007), BBS data are more likely to represent regional bird communities than data that were collected in smaller, less representative sampling frames. Gaining insight into factors influencing regional density and distribution of grassland birds can lead to increased understanding of grassland bird population trends, as well as better planning for the conservation of grassland birds.
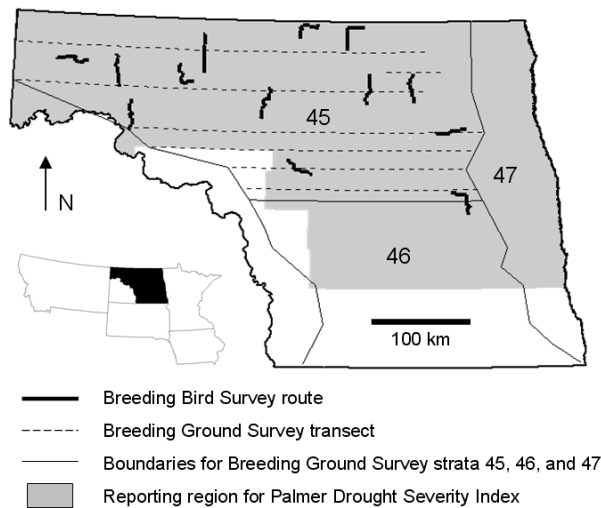
FIGURE 1. Location of Breeding Ground Survey strata 45, 46, and 47 in northeastern North Dakota along with 13 Breeding Bird Survey routes, seven Breeding Ground Survey transects in stratum 45, and Palmer Drought Severity Index reporting area included in analysis.

METHODS

MOISTURE INDICES

May pond indices. Every May, teams of pilots and observers from the U.S. Fish and Wildlife Service's Division of Migratory Bird Management systematically collect data on wetlands and breeding waterfowl along standardized Breeding Ground Survey transects from single-engine, fixed-wing aircraft. We analyzed relationships between numbers of May ponds and grassland birds from 1980 to 2004 in Breeding Ground Survey stratum 45, which is located in northern North Dakota (Fig. 1) and is one of 52 traditional Breeding Ground Survey strata throughout the north-central contiguous United States, Canada, and Alaska (Smith 1995). We selected Breeding Ground Survey stratum 45 because it occurs in the region with the greatest species richness of grassland birds in North America (Peterjohn and Sauer 1999), and BBS data were more complete in stratum 45 than in other strata in the region. We chose not to combine information from several waterfowl survey strata, as pooling data from larger geographical areas could cancel out differences in pond numbers and the subsequent response of grassland birds to changes in moisture levels.

May pond numbers were estimated annually as part of the Breeding Ground Survey. Aerial transects were flown 30–50 m above the ground at approximately 160 km per hour along seven east–west transects. An observer in the aircraft counted Type III (seasonal), IV (semipermanent), and V (permanent) wetlands (Shaw and Fredine 1956) within 200 m of the transect line on the right side of the aircraft. Pond counts were adjusted annually using visibility correction factors derived from subsets of segments sampled at the same time by observers on the ground. Consistent methods were used throughout the survey period, and we treated estimates of May pond numbers as our first index of regional moisture levels.

Palmer Drought Severity Index. We included values from the Palmer Drought Severity Index (PDSI) as a second measure of regional precipitation levels and moisture levels. The PDSI is a widely used, monthly index of soil moisture incorporating measures of moisture supply and demand (PDSI data are available at <http://lwf.ncdc.noaa.gov/oa/ncdc.html>). The index generally ranges from –6 to +6, with negative values indicating dry conditions and positive values indicating wet conditions; values from –0.5 to +0.5 indicate normal conditions. The PDSI data we used were from established geographic reporting divisions comprised of groupings of North Dakota counties. Two entire and three partial PDSI reporting divisions within stratum 45 contained all BBS routes within the stratum; data from these five divisions were strongly correlated (mean $r = 0.76$, range = 0.67–0.84;), so we averaged PDSI data from the geographic divisions, weighting PDSI values by the number of BBS routes ($n = 1$–5) in each division. PDSI values are available for all months of the year, but we selected May values to be consistent with the timing of May pond counts.

BREEDING BIRD DATA

We assessed associations between moisture levels and obligate and facultative species of grassland birds whose numbers have been observed to vary with moisture during local studies in the northern Great Plains (Table 1). We included two wetland species, the Marsh Wren (*Cistothorus palustris*) and Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), as these species are common in the study region, are often associated with grassland-wetland complexes in the region, and their densities have been observed to vary with precipitation (Kroodsma and Verner 1997, Fletcher and Koford 2004). We also included the Brown-headed Cowbird (*Molothrus ater*), hypothesizing that this species' numbers and distribution might be influenced by moisture-related vegetation conditions or by the numbers and distributions of potential hosts.

We used BBS data available electronically from the U.S. Geological Survey's Patuxent Wildlife Research Center (<http://www.pwrc.usgs.gov/bbs/retrieval/menu.cfm>). BBS data were gathered along standardized survey routes (Fig. 1), each of which was 40 km long with 50 designated sample points, or stops, 0.8 km apart. All birds seen or heard within 400 m of each stop were recorded during a 3 min period (Bystrak 1981). The location of BBS routes rarely changes, allowing comparisons to be made among years. Routes were sampled in the same manner during the breeding season (primarily June) each year, although some routes were not sampled every year and some observers changed between years. Because of sampling biases and incomplete detection, the BBS provides a population index, rather than a population estimate (Bystrak 1981), but this index is useful for monitoring trends.

TABLE 1.   Species included in analyses of associations between bird detections and moisture indices in northern North Dakota, 1980–2004, showing previously reported responses to precipitation or moisture and references for reported responses.

Species	Response(s)	Reference(s)[a]
Eastern Kingbird (*Tyrannus tyrannus*)	+ −[b]	4
Horned Lark (*Eremophila alpestris*)	−, +, −	1, 2, 3
Sedge Wren (*Cistothorus platensis*)	+	3
Marsh Wren (*Cistothorus palustris*)	+	5
Sprague's Pipit (*Anthus spragueii*)	+	2
Common Yellowthroat (*Geothlypis trichas*)	+, +	3, 4
Clay-colored Sparrow (*Spizella pallida*)	+, +, −	2, 3, 4
Vesper Sparrow (*Pooecetes gramineus*)	+	2
Lark Bunting (*Calamospiza melanocorys*)	+, −	1, 3
Savannah Sparrow (*Passerculus sandwichensis*)	+, +	3, 4
Grasshopper Sparrow (*Ammodramus savannarum*)	+, +	1, 2
Baird's Sparrow (*Ammodramus bairdii*)	+ −[b]	4
Le Conte's Sparrow (*Ammodramus leconteii*)	+, none	6, 7
Chestnut-collared Longspur (*Calcarius ornatus*)	−	3
Bobolink (*Dolichonyx oryzivorus*)	+, +	3, 4
Western Meadowlark (*Sturnella neglecta*)	−, + −[b]	1, 4
Red-winged Blackbird (*Agelaius phoeniceus*)	+, none	4, 8
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	+	8
Brown-headed Cowbird (*Molothrus ater*)	unknown	none

[a] 1: Wiens (1974); 2: George et al. (1992); 3: Johnson (2005); 4: Cody (1985); 5: Kroodsma and Verner (1997); 6: Igl and Johnson (1999); 7: Winter, Shaffer et al. (2005); 8: Fletcher and Koford (2004).
[b] Cody (1985) reported response to moisture from >1 time period.

For each year from 1980 to 2004, we analyzed BBS data at two levels of response: the mean number of birds of each species detected per route, and the percentage of 13 routes on which each species was detected. We considered the first of these to be a route-level index of abundance and the second to be a regional index of dispersion. Because some BBS routes within the stratum were not sampled every year and some routes encompassed little grassland habitat that could harbor grassland birds, only routes with at least one individual of a target species present were included when calculating

number of birds per route. In instances when no birds of a target species were detected on any of the routes in the stratum, 0 was entered for each level of response. To illustrate the range in variation in numbers among years and species, we calculated the ratio between the minimum and maximum number of individuals detected for each species during the analysis period.

STATISTICAL ANALYSES

We used information-theoretic methods (Burnham and Anderson 1998) to assess support for two hypotheses regarding associations between bird population indices and moisture indices in our study region. First, we considered the hypothesis that abundance and dispersion of breeding birds were influenced by moisture levels observed during the same year that birds were sampled. We used linear regression to investigate this hypothesis by fitting and comparing support for the following three models: 1) a null model of no moisture effect; 2) a model with a linear relationship between abundance and dispersion of birds and May pond numbers in the same year; and 3) a model with a linear relationship between abundance and dispersion of birds and the PDSI in May of the same year. Models 2 and 3 can be described as $Y = \beta_0 + \beta_c(\text{moisture}_c)$, where Y is the bird response (i.e., number of birds or percentage of routes with birds present), β_0 is an intercept term, β_c is a parameter for moisture, and moisture_c is the value of the moisture index (May ponds or PDSI) for the year in which bird data were collected. Second, we considered the hypothesis that abundance and dispersion of breeding birds were influenced by moisture levels from the previous year as well as the same year in which bird data were collected. We investigated this hypothesis by fitting and comparing support for two additional models: 4) a model in which the abundance and dispersion of birds were jointly related to May pond numbers in the year in which bird data were collected and the previous year; and 5) a model in which the abundance and dispersion of birds were jointly related to the PDSI in May of the year in which bird data were collected and the previous year. Models 4 and 5 can be described as $Y = \gamma_0 + \gamma_c(\text{moisture}_c) + \gamma_p(\text{moisture}_p)$, where Y is the bird response, γ_0 is an intercept term, γ_c is a parameter for moisture_c, and γ_p is a parameter for moisture_p, the previous year's moisture index (May ponds or PDSI).

We calculated Akaike's information criterion corrected for small sample size (AIC_c) and Akaike weights (w_i; Burnham and Anderson 1998) for each model. Akaike weights provide an indication of the relative likelihood of competing models best fitting the data; this enabled us to evaluate the strength of evidence for a response to moisture levels, type of moisture index (May ponds vs. PDSI), and timing (same year in which bird data were collected vs. same year and the previous year). To illustrate how much variation in abundance and dispersion was attributable to moisture, we report r^2 values for the model receiving the most support for each species; we report adjusted

R^2 values for those models that included moisture indices from the same year in which bird data were collected and the previous year. To better understand the relationship between the two moisture indices and how birds responded to them, we calculated Spearman's rank correlation between the values of the two moisture indices. We also evaluated temporal autocorrelation of each moisture index by calculating Spearman's rank correlation between the values of each annual moisture index at time lags from one to 10 years. Determining associations at two levels of response for 19 species increased the possibility of spurious results, but also provided the opportunity to assess patterns in response to moisture by many species, which was the goal of our analysis. To reduce the possibility of spurious associations, we only assessed species that were regularly detected on BBS routes in the study area and for which abundance had previously been observed to vary in response to moisture levels (Table 1). Because of a lack of variation in the response variable, we could not determine associations between moisture indices and percentage of routes on which a species was detected for species that were detected on most or all routes throughout the study period. We treat our assessment as an exploratory effort to identify associations and patterns and suggest hypotheses regarding the response of grassland birds to annual moisture levels in the northern Great Plains. We used Number Cruncher Statistical System (Hintze 2004) for all statistical analyses.

RESULTS

The number of May ponds estimated to be present in stratum 45 from 1980 to 2004 ranged from 59 100 in 1991 to 895 500 in 1999 ($\bar{x} = 365\ 400$; Fig. 2); Palmer Drought Severity (PDSI) values during the period ranged from –3.87 (severe drought) in 1980 to 5.09 (extremely wet) in 1999 ($\bar{x} = 0.55$; Fig. 2). Values of the two moisture indices were positively correlated ($r = 0.75$; Fig. 2). Numbers of May ponds were positively

FIGURE 3.   May moisture indices from 1980 to 2004 at time lags ranging from one to 10 years showed (A) positive temporal autocorrelation at time lags of one and two years for number of ponds counted during May waterfowl surveys, and (B) negative temporal autocorrelation at a time lag of six years for the Palmer Drought Severity Index in northern North Dakota. Filled squares represent statistically significant ($|r| > 0.4$) autocorrelation.

correlated with numbers from the previous two years; the correlations of PDSI values with values from previous years showed a similar pattern to those of May pond numbers, although correlations were not as pronounced (Fig. 3). The number of BBS routes surveyed annually in stratum 45 during the study period ranged from six to 13 ($\bar{x} = 10.3$). Mean number of individuals detected annually varied among years and species (Table 2).

Overall, models incorporating the number of May ponds received considerably more support than the null model for explaining variation in abundance of grassland birds in our study region (Table 3; sum of squares error and AIC$_c$ differences [Δ_i] are reported in Appendix A). Responses varied among species, but the data indicated substantial support for moisture influencing abundance of 17 of the 19 study species (Fig. 4) and showed limited support for an influence of moisture on Vesper Sparrow and Baird's Sparrow abundance (Table 3). Models including same-year May pond numbers received more support ($\bar{x}$ of $w_i = 0.38$) than models including same-year PDSI data ($\bar{x}\ w_i = 0.12$) or models also including previous-year May pond numbers ($\bar{x}\ w_i = 0.33$) or previous-year PDSI values ($\bar{x}\ w_i = 0.07$; Table 3).

Ten species were detected on most or all routes throughout the study period and thus could not be included in our analysis of the effects of moisture on species dispersion. For seven of the remaining nine species, models incorporating moisture
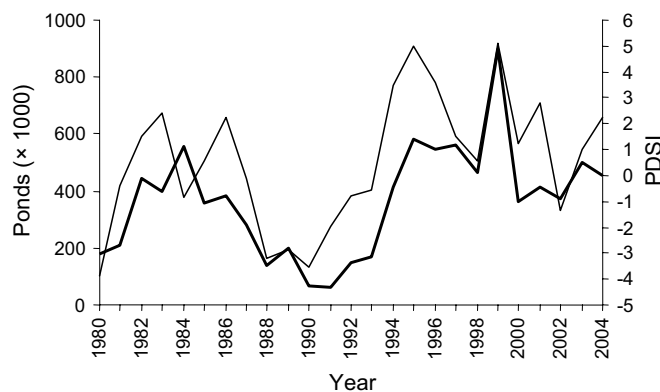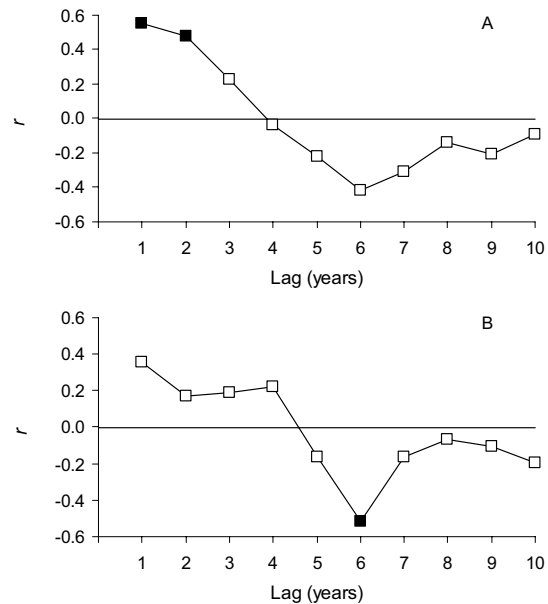

FIGURE 2.   The number of ponds counted during May waterfowl surveys (thick line) and the Palmer Drought Severity Index (thin line) in northern North Dakota, 1980–2004, closely corresponded ($r = 0.75$), with both indicating drier-than-usual conditions in 1988–1993.

TABLE 2.   Mean, minimum, maximum, and the ratio between the minimum and maximum number of birds observed annually per Breeding Bird Survey route in northern North Dakota, 1980–2004.

Species	Mean	Minimum	Maximum	Ratio
Eastern Kingbird	26.3	14.2	46.5	3.3
Horned Lark	94.8	40.6	146.8	3.6
Sedge Wren	5.4	1.0	12.6	12.6
Marsh Wren	13.7	4.3	29.2	6.7
Sprague's Pipit	7.2	2.3	22.5	10.0
Common Yellowthroat	17.7	10.4	24.3	2.3
Clay-colored Sparrow	26.8	10.8	49.5	4.6
Vesper Sparrow	30.0	13.3	45.6	3.4
Lark Bunting	23.9	0.0	103.5	—[a]
Savannah Sparrow	20.2	5.8	38.9	6.7
Grasshopper Sparrow	14.7	5.8	23.2	4.0
Baird's Sparrow	10.5	4.0	20.0	5.0
Le Conte's Sparrow	3.1	0.0	6.8	—[a]
Chestnut-collared Longspur	31.5	16.2	61.8	3.8
Bobolink	20.0	9.3	37.9	4.1
Western Meadowlark	93.9	11.0	160.8	14.6
Red-winged Blackbird	189.9	124.1	270.8	2.2
Yellow-headed Blackbird	124.5	37.6	203.5	5.4
Brown-headed Cowbird	106.6	51.1	172.6	3.4

[a]The ratio between minimum and maximum was not calculated for Lark Bunting and Le Conte's Sparrow, as the minimum number of individuals detected was 0.

indices received more support than the null model for explaining the percentage of routes on which each species was present (Table 4; sum of squares error and AIC_c differences [Δ_i] are reported in Appendix B). The null model received the most support for Sprague's Pipit and Chestnut-collared Longspur. The data indicated that neither moisture index or time period was substantially better than the other for explaining variation in bird dispersion throughout the study area (Table 4).

DISCUSSION

Associations between moisture and the abundance and dispersion of grassland birds in the northern Great Plains have substantial implications for understanding regional populations of these species. Although our analyses were based on observational rather then experimental data, changes in abundance exhibited in BBS data were highly consistent with findings of local, intensive studies. Our results occasionally differed from previous studies, which may be a consequence of shorter time frames in other studies, different methodology (i.e., the use of moisture indices from multiple time periods by Cody [1985]), or differing responses of birds in more arid regions. For example, precipitation generally follows an east–west gradient across the Great Plains, with greater amounts of precipitation in the eastern Great Plains and lower amounts farther west (Wiens 1974). Consequently, grassland birds might respond differently to precipitation levels depending on location; i.e., a

TABLE 3.   Akaike weights for models assessing associations between the mean number of birds detected on Breeding Bird Survey routes and two moisture indices and time periods in northern North Dakota, 1980–2004. The first moisture index, Ponds, was the number of water-filled ponds estimated from annual May waterfowl breeding ground surveys; the Palmer Drought Severity Index (PDSI) was the second moisture index. An asterisk indicates the greatest weight for each row; values in the last row are mean weights for each column. Row totals for Akaike weights may not sum to 1.0 due to rounding. R^2 values indicate the percentage of variation that was explained by moisture levels in the model with the greatest Akaike weight.

Species	Null model	Ponds (same year)	PDSI (same year)	Ponds (same and previous years)	PDSI (same and previous years)	R^2
Eastern Kingbird	0.04	0.45*	0.04	0.45*	0.03	26
Horned Lark	0.02	0.28*	0.25	0.28*	0.17	28
Sedge Wren	0.00	0.65*	0.02	0.31	0.02	44
Marsh Wren	0.00	0.57*	0.00	0.42	0.00	43
Sprague's Pipit	0.15	0.29*	0.18	0.16	0.22	15
Common Yellowthroat	0.14	0.57*	0.11	0.14	0.03	20
Clay-colored Sparrow	0.11	0.37*	0.15	0.29	0.08	18
Vesper Sparrow	0.57*	0.17	0.17	0.05	0.04	—[a]
Lark Bunting	0.00	0.14	0.38*	0.13	0.35	45
Savannah Sparrow	0.01	0.32	0.02	0.60*	0.05	38
Grasshopper Sparrow	0.15	0.43*	0.25	0.11	0.06	17
Baird's Sparrow	0.52*	0.15	0.21	0.05	0.07	—[a]
Le Conte's Sparrow	0.00	0.52*	0.01	0.45	0.02	41
Chestnut-collared Longspur	0.00	0.53*	0.04	0.42	0.01	46
Bobolink	0.05	0.62*	0.12	0.18	0.03	26
Western Meadowlark	0.13	0.21	0.07	0.56*	0.03	22
Red-winged Blackbird	0.00	0.03	0.00	0.97*	0.00	55
Yellow-headed Blackbird	0.02	0.57*	0.04	0.31	0.07	32
Brown-headed Cowbird	0.07	0.34	0.12	0.37*	0.10	29
Mean	0.10	0.38*	0.12	0.33	0.07	32

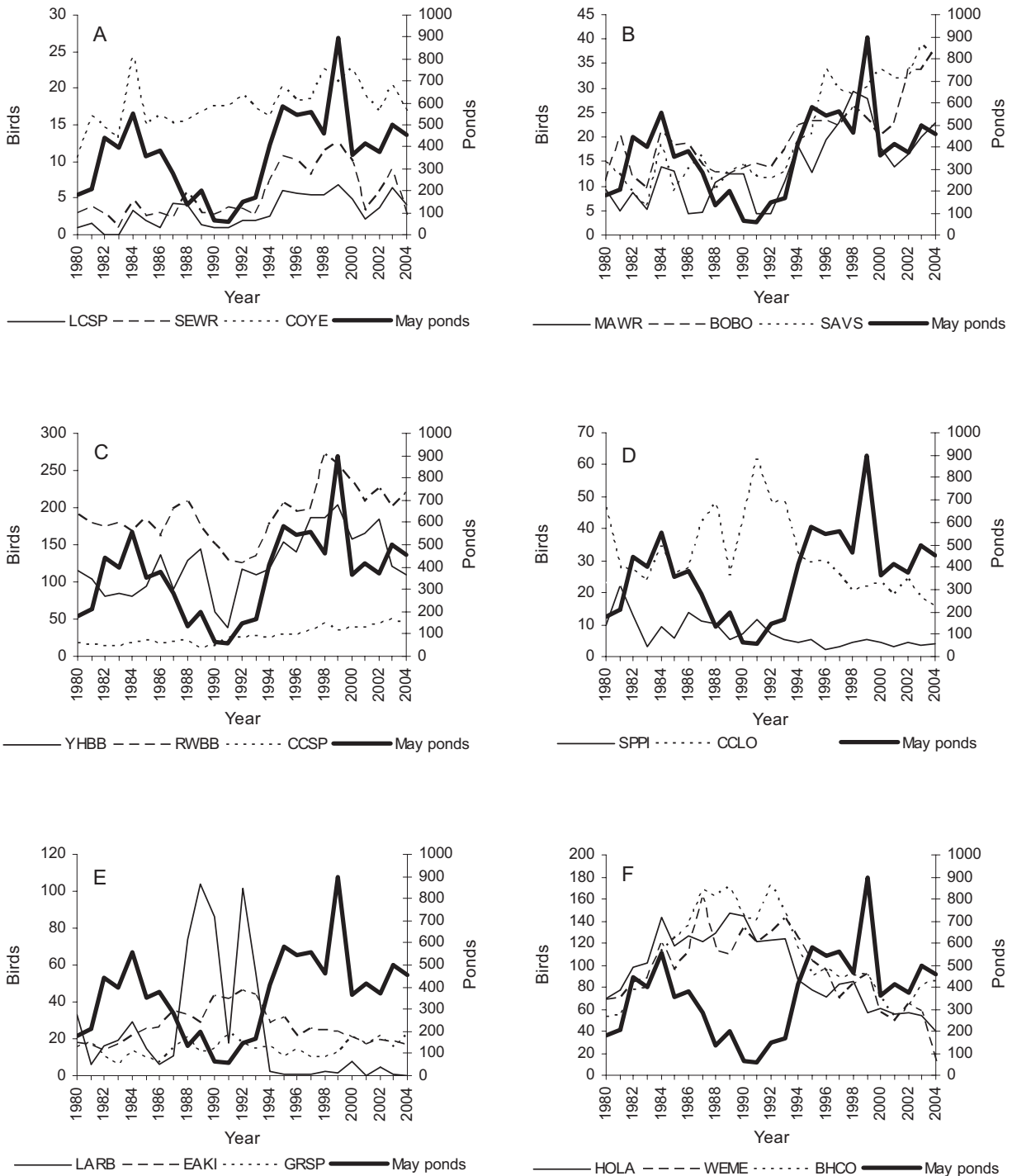[a]R^2 not calculated as the null model had the greatest weight.

FIGURE 4. (A–C) Mean number of individuals detected of nine of 17 grassland bird species were positively associated with number of ponds counted during May waterfowl surveys in northern North Dakota, 1980–2004. LCSP = Le Conte's Sparrow, SEWR = Sedge Wren, COYE = Common Yellowthroat, MAWR = Marsh Wren, BOBO = Bobolink, SAVS = Savanna Sparrow, YHBB = Yellow-headed Blackbird, RWBB = Red-winged Blackbird, CCSP = Clay-colored Sparrow. (D–F) Mean number of individuals detected of eight of 17 grassland bird species were negatively associated with number of May ponds. SPPI = Sprague's Pipit, CCLO = Chestnut-collared Longspur, LARB = Lark Bunting, EAKI = Eastern Kingbird, GRSP = Grasshopper Sparrow, HOLA = Horned Lark, WEME = Western Meadowlark, BHCO = Brown-headed Cowbird. Graphs for Vesper Sparrow and Baird's Sparrow were not included, as weight of evidence suggested that numbers of these species were less influenced by moisture indices. Note different y-axis scales.

TABLE 4.   Akaike weights for models assessing associations between the percentage of routes on which birds were detected and two moisture indices and time periods in northern North Dakota, 1980–2004. The first moisture index, Ponds, was the number of water-filled ponds estimated from annual May waterfowl breeding ground surveys; the Palmer Drought Severity Index (PDSI) was the second moisture index. An asterisk indicates the greatest weight for each row; values in the last row are mean weights for each column. Row totals for Akaike weights may not sum to 1.0 due to rounding. R^2 values indicate the percentage of variation that was explained by moisture levels in the model with the greatest Akaike weight.

Species	Null model	Ponds (same year)	PDSI (same year)	Ponds (same and previous years)	PDSI (same and previous years)	R^2
Sedge Wren	0.07	0.56*	0.15	0.14	0.08	24
Marsh Wren	0.09	0.25	0.40*	0.13	0.12	20
Sprague's Pipit	0.45*	0.24	0.13	0.09	0.09	—[a]
Lark Bunting	0.00	0.09	0.51*	0.07	0.33	53
Savannah Sparrow	0.08	0.32*	0.41	0.08	0.10	19
Grasshopper Sparrow	0.00	0.01	0.01	0.63*	0.35	43
Baird's Sparrow	0.22	0.15	0.38*	0.12	0.13	14
Le Conte's Sparrow	0.07	0.18	0.12	0.11	0.52*	25
Chestnut-Collared Longspur	0.53*	0.14	0.21	0.05	0.07	—[a]
Mean	0.17	0.22	0.26*	0.16	0.20	28

[a] R^2 not calculated as the null model had the greatest weight.

species with a preference for "average" moisture levels might respond positively to increased moisture in drier portions of its range and respond negatively to increased moisture in moister portions of its range. This may be illustrated by the negative association between moisture and Grasshopper Sparrow abundance and dispersion that we observed, which contrasts with the findings of Wiens (1974) and George et al. (1992) in Colorado and western North Dakota, respectively. Similarly, the distribution of a species whose range is primarily east of our study area (e.g., the Sedge Wren) might temporarily shift to the west during wet periods, whereas the distribution of a species whose range is primarily west of our study area (e.g., the Lark Bunting) might temporarily shift to the east during dry periods.

Our results indicate that the response of grassland birds to varying amounts of moisture can be detected at different levels, although support for moisture-related shifts in dispersion was weaker than support for moisture-related changes in numbers. The number of stops on BBS routes at which birds of each species were detected also was correlated with moisture (NDN, unpubl. data), suggesting within-route changes in distribution in addition to the regional changes noted here. Our findings are consistent with observations of changing use of moist and dry sites by grassland birds and regional distribution of grassland birds in the northern Great Plains in response to moisture levels (Kantrud and Faanes 1979, Hubbard 1982).

Species also may be influenced by conditions they encounter on their northward migration. It is possible, as with some waterfowl (Pospahala et al. 1974, Johnson and Grier 1988, Miller and Duncan 1999), that migrating grassland birds seek out areas with suitable moisture levels, which could generate additional patterns across a larger geographic area.

Associations between birds and moisture may be stronger in those portions of the breeding range that birds first encounter on migration within their breeding range, as they might settle on breeding territories if they find conditions are suitable or move on if conditions are not suitable. If overall numbers are stable, geographic shifts in distributions should cancel each other (i.e., lower numbers in one area should correlate with higher numbers in other areas; see also Pospahala et al. 1974, Peterjohn and Sauer 1997).

The mechanisms underlying the patterns we documented are unknown (Igl and Johnson 1999), but likely vary among species and scale of response. Most discussions of the effects of moisture on grassland birds focus on ecological processes such as changes in vegetation, variation in recruitment and productivity, and changes in food supply (Wiens 1974, Cody 1985, Wiens 1989, George et al. 1992). All of these are likely mechanisms for the patterns we described; however, related anthropogenic factors also might influence or confound bird responses to moisture levels. Drought affects agricultural practices, with changes in crops, grazing intensity, and timing of harvest. In addition, fields enrolled in the U.S. Department of Agriculture's Conservation Reserve Program often are released for emergency haying or grazing, which alters the structure of grassland vegetation and likely influences local bird populations (Horn and Koford 2000). We have assumed that species responded independently to the effects of moisture, but given the presence of both positive and negative responses to moisture, interspecific interactions should not be ruled out, particularly in the case of the Brown-headed Cowbird. Whatever the mechanisms, the patterns we documented are of sufficient magnitude that they warrant consideration when evaluating the population status of many species.

Our perception of the response of grassland birds to moisture may be affected by differences between the two indices that we used or confounded by temporal autocorrelation of the moisture indices. Overall, models including May pond numbers in the previous year and the year in which bird data were collected received considerable support for explaining bird abundance. Numbers of May ponds were positively correlated with values from the previous two years, and it is possible that birds were responding to vegetation characteristics influenced by moisture levels in the previous year (or more), as well as conditions in the same year. Given that grassland birds in the northern Great Plains inhabit a variable environment, it is reasonable to assume that they can respond to current weather conditions as well as to vegetation density or structure. Levels of temporal autocorrelation also might explain why most responses showed a stronger association with May pond numbers than with the Palmer Drought Severity Index (PDSI) values, which were not as strongly correlated with previous years' values. Temporal autocorrelation in moisture levels also reinforces the importance of long-term datasets, as short-term studies are likely to have similar moisture levels throughout the study period, making it difficult to detect moisture-influenced changes in abundance, distribution, or reproductive success.

Given the influence of moisture levels on grassland birds in the Great Plains, it may be useful to incorporate moisture indices into regional studies and surveys of grassland bird populations. This may be particularly important for those species exhibiting wide annual variation in abundance. Assuming that the associations between grassland bird abundance and moisture indices are biologically real, models including the number of May ponds received considerably more support than other models for most species, and May ponds would be the preferred index. However, May pond data are not available for most regions in North America. Results of analyses using May pond numbers and the PDSI were similar and correlated, suggesting value in using the PDSI. In addition, the PDSI offers more flexibility because of finer temporal resolution (monthly vs. annual values) and spatial resolution, in addition to being available over a wider geographical area and a longer time period. It may be possible to use PDSI values from >1 time period to better predict grassland bird abundance, but given the risk of spurious correlations from the numerous possible monthly combinations, analysis should be conducted using a priori information on individual species' biology, if it is available. For example, inclusion of information from the previous year may be more appropriate for species that rely heavily on residual vegetation from the previous growing season. Our approach was necessarily coarse-grained and likely obscured fine-grained patterns, as rainfall in our study region is often localized, with corresponding area-specific influences on vegetation and bird communities. Associations between moisture and bird numbers might be more accurately described if sampling and analysis took place using sampling frames at finer resolution (i.e., data for PDSI reporting regions linked to individual studies or BBS routes). The spatial and temporal scales of analysis will likely influence results, as may the types of habitats sampled as habitat use by some species could change with precipitation patterns.

Changes in bird numbers might reflect a shift in distribution, a change in population size caused by altered survival or reproductive success, or both. However, no clear patterns are apparent from the few studies that have examined reproductive success of grassland birds in relation to moisture or climatic conditions in the northern Great Plains. Winter et al. (2005) and Winter, Shaffer et al. (2005) found limited support for moisture influencing density or nesting success of grassland birds; their inability to detect these associations might have been influenced by limited climatic variation during their four-year study, proximity of their three study regions, or by their selection of uniform study sites, which would not reflect variation in habitat and birds present in the entire landscape. Fletcher and Koford (2004) noted that density and reproductive success of wetland-nesting Yellow-headed Blackbirds, but not Red-winged Blackbirds (*Agelaius phoeniceus*), were positively correlated with water levels; however, clutch size was reduced and nest initiation was delayed in dry years for both species. Yackel Adams et al. (2006) found that survival of postfledging Lark Buntings in Colorado was negatively associated with drought intensity. In shrub habitats of the western United States, reproductive success of Sage Sparrows (*Amphispiza belli*), Brewer's Sparrows (*Spizella breweri*), and Rufous-crowned Sparrows (*Aimophila ruficeps*) was positively associated with precipitation (Rotenberry and Wiens 1991, Morrison and Bolger 2002). Associations between moisture and reproductive success have been linked to food availability and predator activity (Rotenberry and Wiens 1991, Morrison and Bolger 2002, Fletcher and Koford 2004, Yackel Adams et al. 2006). High environmental variation may well influence survival or reproductive success of grassland birds in the Great Plains; understanding how these associations interact with conservation and management activities is needed to ensure the effectiveness of grassland bird conservation efforts in the region.

Our results provide additional insight into the high variation in grassland bird populations often observed in the Great Plains and corroborate findings from shorter-term studies. Over long time periods or large geographic areas, this variation will likely not greatly affect population trend estimates. However, over shorter time periods, local population changes caused by varying moisture levels (Igl and Johnson 1999, Peterjohn and Sauer 1999) may confound regional perceptions of population trend and status. Also, variation in bird numbers should be considered when conservation goals are set

and when the effects of conservation actions are assessed for grassland birds in the northern Great Plains. Over the longer term, our results suggest that changes in precipitation levels and patterns predicted by some global climate change models will affect the distribution and abundance of grassland bird species in the region (Price 1995, Matthews et al. 2004). Presently, landscape-level habitat models (Niemuth et al. 2005, Reynolds et al. 2006) are used for identifying and prioritizing grassland habitat for conservation in the northern Great Plains, but managers must recognize that presence and numbers of many grassland bird species at priority sites can fluctuate widely depending on local and regional moisture levels. Our results emphasize the importance of maintaining a variety of grassland and wetland complexes embedded in suitable landscapes across broad regions, ready to meet the varying needs of different species of grassland birds under differing moisture regimes. The high temporal and spatial variation in abundance and dispersion of grassland birds evident in BBS data reinforces the importance of broad spatial extents and long time frames in understanding and conserving grassland bird populations in the northern Great Plains.

ACKNOWLEDGMENTS

LITERATURE CITED

ALISAUSKAS, R. T., AND T. W. ARNOLD. 1994. American Coot, p. 127–143. *In* T. C. Tacha and C. E. Braun [EDS.], Migratory shore and upland game bird management in North America. International Association of Fish and Wildlife Agencies, Washington, DC.

ASKINS, R. A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. Current Ornithology 11:1–34.

BRAGG, T. B. 1995. The physical environment of Great Plains grasslands, p. 49–81. *In* A. Joern and K. H. Keeler [EDS.], The changing prairie: North American grasslands. Oxford University Press, New York.

BREWSTER, W. G., J. M. GATES, AND L. D. FLAKE. 1976. Breeding waterfowl populations and their distribution in South Dakota. Journal of Wildlife Management 40:50–59.

BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

BYSTRAK, D. 1981. The North American Breeding Bird Survey. Studies in Avian Biology 6:34–41.

CODY, M. L. 1985. Habitat selection in grassland and open-country birds, p. 191–226. *In* M. L. Cody [ED.], Habitat selection in birds. Academic Press, New York.

FLETCHER, R. J., JR., AND R. R. KOFORD. 2004. Consequences of rainfall variation for breeding wetland blackbirds. Canadian Journal of Zoology 82:1316–1325.

GEORGE, T. L., A. C. FOWLER, R. L. KNIGHT, AND L. C. MCEWEN. 1992. Impacts of a severe drought on grassland birds in western North Dakota. Ecological Applications 2:275–284.

HINTZE, J. 2004. NCSS and PASS. Number Cruncher Statistical Systems, Kayesville, UT.

HORN, D. J., AND R. R. KOFORD. 2000. Relation of grassland bird abundance to mowing of Conservation Reserve Program fields in North Dakota. Wildlife Society Bulletin 28:653–659.

HUBBARD, D. E. 1982. Breeding birds in two dry wetlands in eastern South Dakota. Prairie Naturalist 14:6–8.

IGL, L. D., AND D. H. JOHNSON. 1999. Le Conte's Sparrows breeding in Conservation Reserve Program fields: precipitation and patterns of population change. Studies in Avian Biology 19:178–186.

JOHNSON, D. H. 2005. Grassland bird use of Conservation Reserve Program fields in the Great Plains, p. 17–32. *In* J. B. Haufler [ED.], Fish and wildlife benefits of Farm Bill conservation programs: 2000–2005 update. The Wildlife Society Technical Review 05-02, The Wildlife Society, Bethesda, MD.

JOHNSON, D. H., AND J. W. GRIER. 1988. Determinants of breeding distributions of ducks. Wildlife Monographs 100:1–37.

KANTRUD, H. A., AND C. A. FAANES. 1979. Range expansion of Baird's Sparrow in South Dakota. Prairie Naturalist 11:111–112.

KROODSMA, D. E., AND J. VERNER. 1997. Marsh Wren (*Cistothorus palustris*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 308. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

MATTHEWS, S. N., R. J. O'CONNOR, L. R. IVERSON, AND A. M. PRASAD. 2004. Atlas of climate change effects in 150 bird species of the eastern United States. USDA Forest Service General Technical Report NE-318.

MILLER, M. R., AND D. C. DUNCAN. 1999. The Northern Pintail in North America: status and conservation needs of a struggling population. Wildlife Society Bulletin 27:788–800.

MORRISON, S. A., AND D. T. BOLGER. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. Oecologia 133:315–324.

NIEMUTH, N. D., A. L. DAHL, M. E. ESTEY, AND C. R. LOESCH. 2007. Representation of landcover along Breeding Bird Survey routes in the northern Plains. Journal of Wildlife Management 71:2258–**2265.**

NIEMUTH, N. D., M. E. ESTEY, AND C. R. LOESCH. 2005. Developing spatially explicit habitat models for grassland bird conservation planning in the Prairie Pothole region of North Dakota, p. 469–477. *In* C. J. Ralph and T. D. Rich [EDS.], Bird conservation implementation and integration in the Americas: Proceedings of the Third International Partners in Flight conference 2002. USDA Forest Service General Technical Report PSW-GTR-191.

NIEMUTH, N. D., AND J. W. SOLBERG. 2003. Response of waterbirds to number of wetlands in the Prairie Pothole region of North Dakota, U.S.A. Waterbirds 26:233–238.

PALMER, W. C. 1965. Meteorological drought. Research Paper No. 45. U.S. Weather Bureau, NOAA Library and Information Services Division, Washington, DC.

PETERJOHN, B. G., AND J. R. SAUER. 1997. Population trends of Black Terns from the North American Breeding Bird Survey, 1966–1996. Colonial Waterbirds 20:566–573.

PETERJOHN, B. G., AND J. R. SAUER. 1999. Population status of North American grassland birds from the North American Breeding Bird Survey 1966–1996. Studies in Avian Biology 19:27–44.

POSPAHALA, R. S., D. R. ANDERSON, AND C. J. HENNY. 1974. Population ecology of the Mallard: II. Breeding habitat conditions, size of the breeding populations, and production indices. U.S. Fish and Wildlife Service Resource Publication 115, Washington, DC.

PRICE, J. T. 1995. Potential impacts of global climate change on the summer distributions of some North American grassland birds. Ph.D. dissertation, Wayne State University, Detroit, MI.

REYNOLDS, R. E., T. L. SHAFFER, C. R. LOESCH, AND R. R. COX JR. 2006. The Farm Bill and duck production in the Prairie Pothole region: increasing the benefits. Wildlife Society Bulletin 34:963–974.

ROTENBERRY, J. T., AND J. A. WIENS. 1991. Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. Ecology 72:1325–1335.

SHAW, S. P., AND C. G. FREDINE. 1956. Wetlands of the United States. U.S. Fish and Wildlife Service Circular 39, Washington, DC.

SMITH, G. W. 1995. A critical review of the aerial and ground surveys of breeding waterfowl in North America. U.S. Department of Interior, National Biological Service Science Report 5, Washington, DC.

SMITH, R. I. 1970. Response of pintail breeding populations to drought. Journal of Wildlife Management 34:943–946.

STEWART, R. E., AND H. A. KANTRUD. 1973. Ecological distribution of breeding waterfowl populations in North Dakota. Journal of Wildlife Management 37:39–50.

WIENS, J. A. 1974. Climatic instability and the "ecological saturation" of bird communities in North American grasslands. Condor 76:385–400.

WIENS, J. A. 1989. The ecology of bird communities. Vol. 2: Processes and variations. Cambridge University Press, Cambridge, UK.

WINTER, M., D. H. JOHNSON, AND J. A. SHAFFER. 2005. Variability in vegetation effects on density and nesting success of grassland birds. Journal of Wildlife Management 69:185–197.

WINTER, M., J. A. SHAFFER, D. H. JOHNSON, T. M. DONOVAN, W. D. SVEDARSKY, P. W. JONES, AND B. R. EULISS. 2005. Habitat and nesting of Le Conte's Sparrows in the northern tallgrass prairie. Journal of Field Ornithology 76:61–71.

WOODHOUSE, C. A., AND J. T. OVERPECK. 1998. 2000 years of drought variability in the central United States. Bulletin of the American Meteorological Society 79:2693–2714.

YACKEL ADAMS, A. A., S. K. SKAGEN, AND J. A. SAVIDGE. 2006. Modeling post-fledging survival of Lark Buntings in response to ecological and biological factors. Ecology 87:178–188.

APPENDIX A.   Sum of squares error (SSE) and difference in Akaike's information criterion corrected for small sample size (Δ_i) for models assessing associations between number of birds detected on Breeding Bird Survey routes and two moisture indices and time periods in northern North Dakota, 1980–2004. The first moisture index, Ponds, was the number of water-filled ponds estimated from annual May waterfowl breeding ground surveys; the Palmer Drought Severity Index (PDSI) was the second moisture index. Number of parameters (K) was two for the null model, three for same-year models, and four for combined-year models. Sample size was 25 for all models.

Species	Null model		Ponds (same year)		PDSI (same year)		Ponds (same and previous years)		PDSI (same and previous years)	
	SSE	Δ_i	SSE	Δ_i	SSE	Δ_i	SSE	Δ_i	SSE	Δ_i
Eastern Kingbird	2190	5.04	1614	0.01	1942	4.64	1439	0.00	1804	5.65
Horned Lark	25 600	5.60	18 443	0.00	18 605	0.22	16 465	0.02	17 090	0.95
Sedge Wren	272	12.05	151	0.00	199	6.85	143	1.45	180	7.17
Marsh Wren	1286	11.55	730	0.00	1095	10.12	668	0.62	1024	11.30
Sprague's Pipit	518	1.39	442	0.00	459	0.98	412	1.15	403	0.59
Common Yellowthroat	234	2.84	188	0.00	214	3.25	187	2.75	212	5.80
Clay-colored Sparrow	3066	2.35	2516	0.00	2700	1.76	2289	0.49	2523	2.93
Vesper Sparrow	1655	0.00	1646	2.46	1641	2.39	1625	5.00	1637	5.18
Lark Bunting	26 256	12.33	15 645	1.98	14 454	0.00	14 067	2.18	12 994	0.20
Savannah Sparrow	2553	8.60	1714	1.24	2103	6.35	1455	0.00	1773	4.94
Grasshopper Sparrow	542	2.09	449	0.00	470	1.11	447	2.71	470	3.95
Baird's Sparrow	373	0.00	372	2.49	362	1.86	363	4.73	353	4.04
Le Conte's Sparrow	105	10.74	61	0.00	84	7.94	55	0.28	70	6.18
Chestnut-collared Longspur	3343	13.00	1791	0.00	2207	5.22	1627	0.46	2184	7.82
Bobolink	1318	5.04	971	0.00	1110	3.34	957	2.49	1095	5.86
Western Meadowlark	20 789	2.97	17 989	1.95	19 663	4.17	14 843	0.00	18 600	5.64
Red-winged Blackbird	31 704	16.58	19 623	7.19	27 151	15.30	13 131	0.00	21 642	12.49
Yellow-headed Blackbird	42 318	7.17	28 633	0.00	35 567	5.42	26 804	1.21	30 218	4.20
Brown-headed Cowbird	36 738	3.24	29 245	0.14	31 797	2.23	25 942	0.00	28 842	2.65

APPENDIX B.   Sum of squares error (SSE) and difference in Akaike's information criterion corrected for small sample size (Δ_i) for models assessing associations between percentage of routes on which birds were detected and two moisture indices and time periods in northern North Dakota, 1980–2004. The first moisture index, Ponds, was the number of water-filled ponds estimated from annual May waterfowl breeding ground surveys; the Palmer Drought Severity Index (PDSI) was the second moisture index. Number of parameters (K) was two for the null model, three for same-year models, and four for combined-year models. Sample size was 25 for all models.

Species	Null model		Ponds (same year)		PDSI (same year)		Ponds (same and previous years)		PDSI (same and previous years)	
	SSE	Δ_i	SSE	Δ_i	SSE	Δ_i	SSE	Δ_i	SSE	Δ_i
Sedge Wren	7066	4.24	5376	0.00	5971	2.62	5357	2.77	5613	3.94
Marsh Wren	7680	2.90	6400	0.94	6165	0.00	6031	2.31	6041	2.35
Sprague's Pipit	2874	0.00	2724	1.26	2870	2.56	2620	3.14	2633	3.27
Lark Bunting	13 609	16.24	7393	3.58	6406	0.00	6698	3.97	5919	0.88
Savannah Sparrow	1890	3.16	1531	0.49	1501	0.00	1531	3.35	1494	2.74
Grasshopper Sparrow	4579	10.95	3630	7.74	3819	9.01	2376	0.00	2491	1.18
Baird's Sparrow	5492	1.06	5102	1.81	4745	0.00	4639	2.29	4619	2.18
Le Conte's Sparrow	14 116	3.93	11 840	2.13	12 224	2.93	10 947	3.03	9697	0.00
Chestnut-collared Longspur	2732	0.00	2731	2.59	2653	1.86	2633	4.53	2591	4.13