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

NEAL D. NIEMUTH[1]

[1]Habitat and Population Evaluation Team

U.S. Fish and Wildlife Service

3425 Miriam Avenue

Bismarck, ND 58501 USA

Email: Neal_Niemuth@fws.gov

JOHN W. SOLBERG[2]

[2]Division of Migratory Bird Management

U.S. Fish and Wildlife Service

3425 Miriam Avenue

Bismarck, ND 58501 USA

TERRY L. SHAFFER[3]

[3]Northern Prairie Wildlife Research Center

U.S. Geological Survey

8711 37th Street SE

Jamestown, ND 58401 USA

Abstract. High annual variation in grassland bird populations in the Great Plains often is attributed to changes in moisture conditions, but most previous assessments of variation in grassland bird numbers were of short duration, occurred during a limited range of moisture conditions, were limited in geographic scope, considered few species, or 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 and populations of 17 species of grassland passerines and 2 species of wetland passerines in northern North Dakota from 1980-2004. We used data from 13 Breeding Bird Survey routes to provide indices of bird abundance and distribution; we used numbers of May ponds from annual 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 abundance of 17 of the 19 species we considered. Models including current-year May pond numbers were generally most strongly associated with variation in bird numbers, followed by models including both current-year and previous-year May pond numbers. Models including PDSI data generally received less support. The distribution of 7 species was influenced by moisture conditions, although the response was not as universal and support was not as strong as it was with abundance. Neither moisture index or time period was substantially superior to the other for explaining variation in bird distribution. Associations between grassland birds and moisture conditions suggest the value of regional moisture indices to interpreting studies and surveys of grassland birds in the northern Great Plains. High temporal and spatial variation in abundance and distribution of grassland birds reinforces the importance of broad spatial extents and long timeframes in understanding and conserving grassland birds in the northern Great Plains.

Key words: climate, grassland bird, North American Breeding Bird Survey, moisture, North Dakota, population dynamics, Prairie Pothole Region, precipitation.

INTRODUCTION

The Great Plains of North America is 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, Johnson and Grier 1988, Brewster et al. 1976) 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 is poorly understood, although many studies report substantial annual variation in numbers of grassland birds in response to moisture conditions or precipitation. Wiens (1974) reported that the density of Horned Lark (see Table 1 for scientific names of species included in analysis) in eastern Colorado was higher during a drought year than a year with higher precipitation, whereas densities of Western Meadowlark, Lark Bunting and Grasshopper Sparrow decreased. George et al. (1992) found that densities of Horned Lark, Sprague's Pipit, Vesper Sparrow, Grasshopper Sparrow, Clay-colored Sparrow, and Field Sparrow (*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 Sparrow 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 that CRP study, densities of Northern Harrier, Sedge Wren, Savannah Sparrow, and Le Conte's Sparrow were higher during a drought in1990-1991 than during a wet period in 1995-1996; conversely, densities of Horned Lark, Chestnut-collared Longspur, and Lark Bunting declined between the two periods (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.

However, the aforementioned observations were incidental to ongoing studies that were not designed to examine the response of bird populations to changes in precipitation and 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 regional bird populations 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 birds 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). Understanding 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 conditions over a 25-year period in northern North Dakota. Our analyses had two primary goals. First, we assessed weight of evidence for associations between grassland birds and current-year moisture conditions as represented by number of May ponds (collected by the U.S. Fish and Wildlife Service) and the Palmer Drought Severity Index (PDSI). This enabled us to determine if grassland bird data from the BBS revealed responses to precipitation similar to those identified by intensive local studies as well as 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 conditions at the time of settling or cues such as condition of residual vegetation that were likely influenced by the previous year's moisture conditions (i.e., lag effect). Our analyses address some of the shortcomings 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 landcover 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. Our analyses provide insights into factors influencing regional density and distribution of grassland birds, which can lead to increased understanding of grassland bird population trends, as well as better planning for the conservation of grassland birds.

METHODS

MOISTURE INDICES

May Pond Indices. Every May, teams of pilot-biologists 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 (BGS) transects from single-engine, fixed-wing aircraft. We analyzed relationships between wetland numbers and grassland birds from 1980-2004 in BGS Stratum 45, which is located in northern North Dakota (Fig. 1) and is one of 52 traditional BGS strata throughout the north-central contiguous United States, Canada, and Alaska (Smith 1995). We selected BGS Stratum 45 as 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 other strata in the region. We chose not to combine information from several waterfowl survey strata, as pooling data from larger geographic areas could average out differences in pond numbers and the subsequent response of grassland birds to changes in moisture conditions.

May pond numbers were estimated annually as part of the BGS. Aerial transects comprised of 29-km segments were flown 30-50 m above the ground at approximately 160 km/h 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 ground observers. Consistent methods were used throughout the survey period, and we treat estimates of May pond numbers as an index to regional moisture conditions.

Palmer Drought Severity Index. We included values from the PDSI as a second measure of regional precipitation levels and moisture conditions. The PDSI is a widely used (available at www1.ncdc.noaa.gov/pub/data/cirs/), monthly index of soil moisture incorporating measures of moisture supply and demand. 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 (range of r = 0.67–0.84; mean r = 0.76), so we averaged PDSI data from the geographic divisions, weighting PDSI values by the number of BBS routes (*n* = 1 to 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 precipitation and obligate and facultative species of grassland birds whose numbers have been observed to vary with precipitation on local studies in the northern Great Plains (Table 1). We included two wetland species, Marsh Wren and Yellow-headed Blackbird, 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). Finally, we also included Brown-headed Cowbird, hypothesizing that their numbers and distribution might be influenced by moisture-related vegetation conditions or track 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.mp2-pwrc.usgs.gov/bbs/retrieval/menu.cfm). BBS data were gathered along standardized survey routes, each of which was 40 km long with 50 designated sample points, or stops, 0.8 km apart (Fig. 1). All birds seen or heard within 400 m of each stop were recorded during a 3-minute 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.

For each year from 1980-2004, we analyzed BBS data at two levels of response: the mean number of birds of each species detected per route and percent of 13 routes on which each species was detected. We consider the first of these to be a route-level index of abundance and the second to be an index of regional distribution. 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 derived from BBS data and moisture indices in our study region. First, we considered the hypothesis that abundance and distribution of breeding birds were influenced by current moisture conditions. We used linear regression to investigate this hypothesis by fitting and comparing support for the following three models: 1) null model of no moisture effect; 2) abundance and distribution of birds was linearly related to May pond numbers in the same year; and 3) abundance and distribution of birds was linearly related to PDSI in May of the same year. Models 2 and 3 can be described as Y = $\hat{\beta}_0 + \hat{\beta}_c(\text{moisture}_c)$, where Y is the bird response (i.e., number of birds or percentage of routes), $\hat{\beta}_0$ is an intercept term, $\hat{\beta}_c$ is a coefficient estimate for a linear model, and moisture_c is the value for the current year's moisture index (May ponds or PDSI). Second, we considered the hypothesis that abundance and distribution of breeding birds were influenced by moisture conditions from the previous year as well as the current year. We investigated this hypothesis by fitting and comparing support for two additional models: 4) abundance and distribution of birds was jointly related to May pond numbers in the current and previous year; and 5) abundance and distribution of birds jointly related to PDSI in May of the current and previous year. Models 4 and 5 can be described as Y = $\hat{\beta}_0 + \hat{\beta}_c(\text{moisture}_c) + \hat{\beta}_p(\text{moisture}_p)$, where Y is the bird response, $\hat{\beta}_c$ and moisture_c are a coefficient estimate and moisture index as described above, and $\hat{\beta}_p$ is a coefficient estimate for a linear model related to moisture_p, which is the value for 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 provided 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 conditions, type of moisture index (May ponds vs. PDSI), and timing (current year vs. current and previous year). To illustrate how much variation in abundance and distribution 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 current and previous year. To better understand the relationship between the two moisture indices and how birds respond to them, we calculated Spearman's rank correlation between values of the two moisture indices. We also evaluated temporal autocorrelation of each moisture index by calculating Spearman's rank correlation between values of each annual moisture index at lags from 1 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 is the emphasis of our paper. To reduce the possibility of spurious associations, we included in analysis only those 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 conditions (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 the analysis as an exploratory effort to identify associations and patterns and suggest hypotheses regarding the response of grassland birds to annual moisture conditions 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 1980-2004 ranged from 59,100 in 1991 to 895,500 in 1999 ($\bar{x}$ = 365,400; Fig. 2); 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 correlated with numbers from the previous two years; correlations of PDSI values with values from previous years showed a similar pattern to those of May pond numbers (Fig. 3). The number of BBS routes surveyed annually in the stratum during the period ranged from 6 to 13 ($\bar{x}$ = 10.3). Mean number of individuals detected annually varied among years and species (Table 2, Fig. 4).

Overall, models incorporating 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, number of parameters, and AIC_c differences [Δ_i] reported in Appendix A). Response varied among species, but the data indicate substantial support for moisture influencing abundance of 17 of the 19 species (Fig. 4) and limited ($w_i \leq 0.21$) support for Vesper Sparrow and Baird's Sparrow (Table 3). Models including current-year May pond numbers received more support ($\bar{x}$ of $w_i = 0.38$) than models including current-year PDSI data ($\bar{x}$ = 0.12) or models also including previous-year May pond numbers ($\bar{x}$ = 0.33) or previous-year PDSI values ($\bar{x}$ = 0.07; Table 3).

Ten species were detected on most or all routes throughout the study period and thus had no variation in presence on routes to model. For seven of the remaining nine species, models incorporating moisture 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, number of parameters, and AIC_c differences [Δ_i] reported in Appendix B). However, models including numbers of May ponds received some support ($w_i \geq 0.21$) for a moisture effect for Sprague's Pipit and Chestnut-collared Longspur, for which the null model received the most support. The data indicate that neither moisture index or time period was substantially better than the other for explaining variation in bird distribution (Table 4).

DISCUSSION

Associations between moisture and the abundance and distribution 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 as exhibited in BBS data were highly consistent with findings of local, intensive studies and the biology of the species involved. Occasional differences in response of birds to moisture (Table 1, Fig. 4) may be a consequence of short time frames in other studies, different methodology, such as Cody's (1985) use of moisture indices from multiple time periods, or differing responses of birds in more arid regions (e.g., Wiens 1974). 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 bird species with a preference for "average" moisture conditions might respond positively to increased moisture in drier portions of its range and respond negatively to increased moisture in moister portions of its range (see also Cody 1985). Similarly, the distribution of species whose range is primarily east of our study area (e.g., Sedge Wren) might temporarily shift to the west during wet periods, whereas the distribution of species whose range is primarily west of our study area (e.g., Lark Bunting) might temporarily shift to the east during dry periods.

Our results indicate that the response of grassland birds to moisture conditions can be detected at different levels, although support for moisture-related shifts in distribution was weaker than support for moisture-related changes in numbers. The number of stops on 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 conditions (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 conditions, and that distribution and abundance throughout the region shift annually relative to moisture. If this is the case, additional patterns may be present 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 ("short-stopping") or move on if conditions are not suitable. If overall numbers are stable, geographic shifts in distributions should balance out (i.e., low 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 moisture effects 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 these are likely mechanisms for the patterns we described; however, related anthropogenic factors also might influence or confound bird responses to moisture conditions. 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 CRP often are released for emergency haying or grazing, which alters structure of grassland vegetation and likely influences local bird populations (e.g., Horn and Koford 2000). We have assumed that species responded independently to moisture effects, but given the presence of both positive and negative responses to moisture, interspecific interactions should not be ruled out, particularly in the case of Brown-headed Cowbird. Whatever the mechanisms, the patterns we documented suggest some consistency in response to moisture conditions and are of sufficient magnitude that they warrant consideration when evaluating population status of many species.

Our perception of the response of grassland birds to moisture may be affected by differences between the two indices or confounded by temporal autocorrelation of moisture indices. Overall, models including current and the previous year's May pond numbers 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 the moisture conditions in the previous year (or more), as well as conditions in the current year. Given that 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 PDSI values, which were not as strongly correlated with previous years' values. Temporal autocorrelation in moisture conditions also reinforces the importance of long-term datasets, as short-term studies are likely to have similar moisture conditions, making it difficult to detect moisture-influenced changes in abundance, distribution, or reproductive success.

Given the influence of moisture conditions on grassland birds in the Great Plains, it may be useful to incorporate regional 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 geographic 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. Our approach was necessarily coarse-grained and likely obscured fine-grained patterns, as rainfall in our study region is often localized, with local influences on vegetation and bird communities.

Associations between moisture and birds likely would be more accurately described if sampling and analysis took place using sampling frames at finer resolution (i.e., data for PDSI reporting regions could be 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 might change with precipitation patterns.

Changes in bird numbers might reflect a shifting of individuals, 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 nesting success of grassland birds in relation to moisture or climatic conditions in the northern Great Plains. Winter et al. (2005a, b) 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 4-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, were positively correlated with water levels; clutch size was reduced and nest initiation was delayed in dry years for both species. In shrub habitats of the western United States, reproductive success of Sage Sparrow (*Amphispiza belli*), Brewer's Sparrow (*Spizella breweri*), and Rufous-crowned Sparrow (*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). High environmental variation may well influence survival and/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, as well as corroborate findings from shorter-term studies. Over long time periods or larger geographic areas, this variation will likely average out and not greatly affect population trend estimates. However, over shorter time periods, local population changes caused by varying moisture conditions (see 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 distribution and abundance of grassland bird species in the region (see also Price 1995, Matthews et al. 2004). Presently, landscape-level habitat models (e.g., 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 conditions. 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 distribution of grassland birds evident in BBS data reinforces the importance of broad spatial extents and long timeframes in understanding and conserving grassland bird populations in the northern Great Plains.

ACKNOWLEDGMENTS

We thank M. Defley, E. Ferguson, M. Hawkes, T. Heuer, M. Laws, D. Ledford, J. Nelson, A. Novara, M. Oliver, J. Peterson, C. Smith, and B. Thrune for assistance in collecting BGS data; J. Bladen for providing archived data; and L. D. Igl, W. E. Newton, and R. E. Reynolds for providing helpful comments on earlier drafts of this paper. We also thank the U.S. Geological Survey for providing BBS data and the many volunteers who survey BBS routes each year in North Dakota, particularly G. B. Berkey, E. E. Freeberg, P. C. Hart, A. Lagasse, J. M. Legge, R. E. Martin, R. K. Murphy, and R. L. Rytter.

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., and J. W. Grier. 1988. Determinants of breeding distributions of ducks. Wildlife Monographs 100:1–37

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.

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. Academy of Natural Sciences, Philadelphia, PA, and 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. Gen. Tech. Rep. NE-318. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, Pennsylvania. 340 pages.

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 PSW-GTR-191, Albany, CA.

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.

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 1996–1996. 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.

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, Michigan.

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. Volume 2: Processes and variations. Cambridge University Press, Cambridge, UK.

Winter, M., D. H. Johnson, and J. A. Shaffer. 2005a. 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. 2005b. 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.

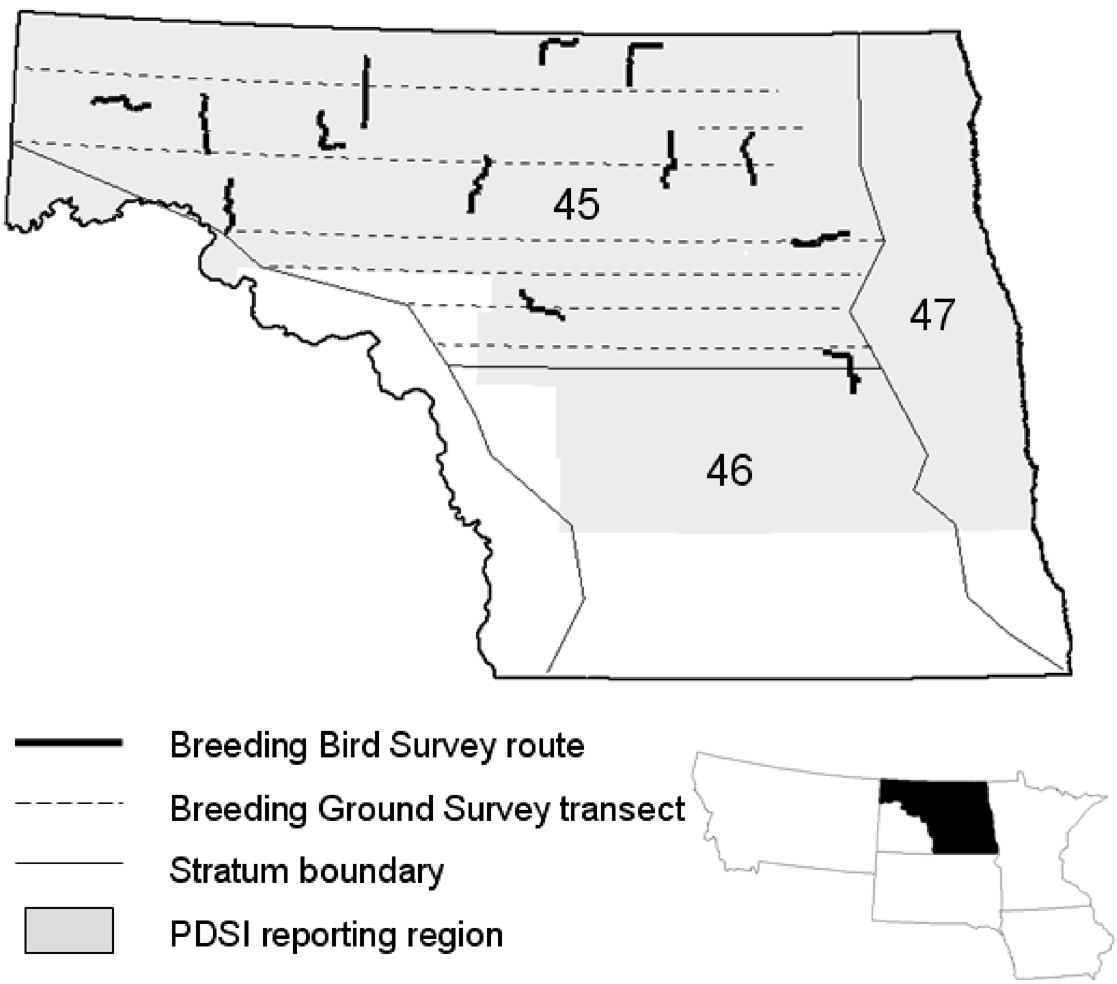
Figure Legends.

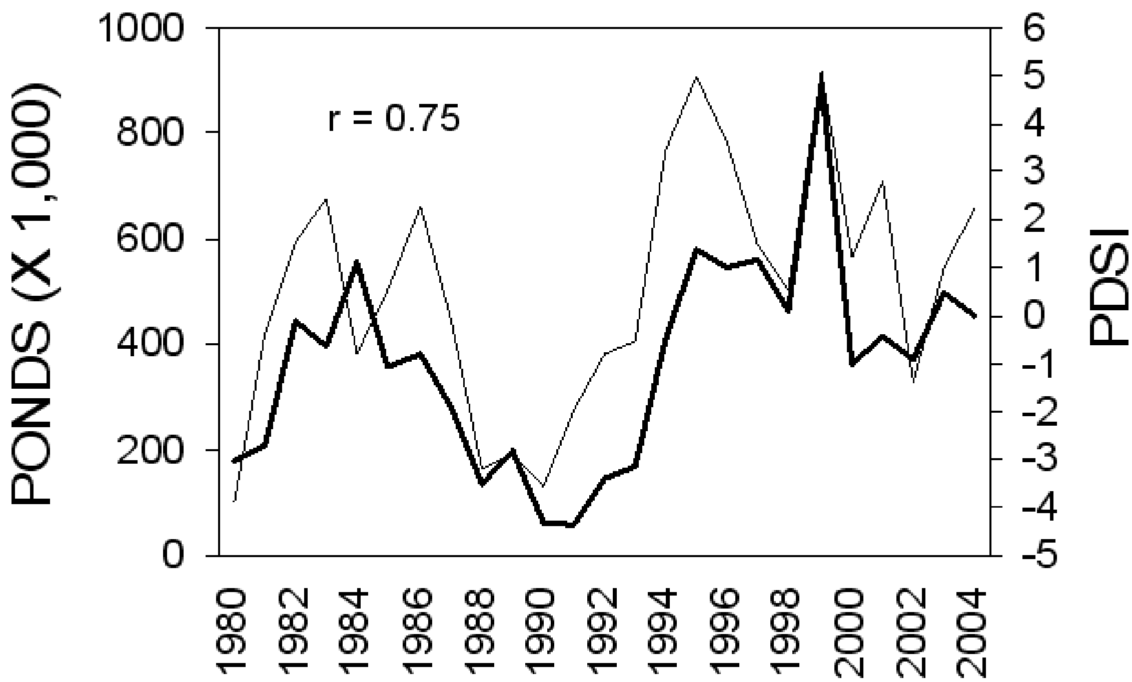
FIGURE 1. Location of Breeding Ground Survey (BGS) strata 45, 46, and 47 in northeastern North Dakota along with 13 Breeding Bird Survey routes, 7 BGS transects in Stratum 45, and PDSI reporting area included in analysis.

FIGURE 2. Number of May ponds (thick line) and Palmer Drought Severity Index (thin line) in northern North Dakota, 1980-2004.

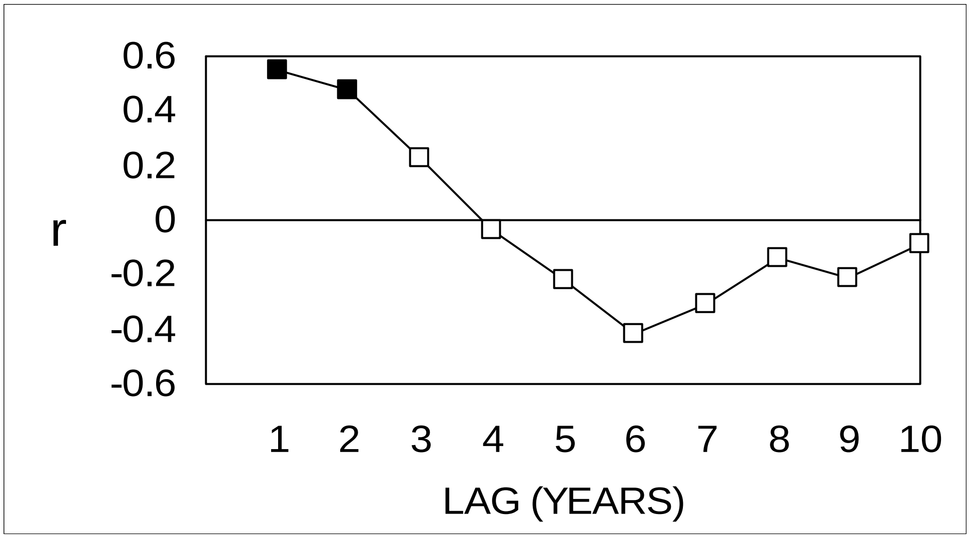
FIGURE 3. Autocorrelation between May moisture indices from 1980-2004 at time lags ranging from 1 to 10 years for (A) number of May ponds and (B) Palmer Drought Severity Index in northern North Dakota. Filled squares represent statistically significant ($|r| > 0.4$) autocorrelation.

FIGURE 4. (A-C) Mean number of individuals detected for grassland bird species that were positively associated with number of May ponds in northern North Dakota, 1980-2004. (D-F) Mean number of individuals detected for grassland bird species that were negatively associated with number of May ponds. Graphs for Vesper Sparrow and Baird's Sparrow were not included, as weight of evidence suggested numbers of these species were less influenced by moisture indices.

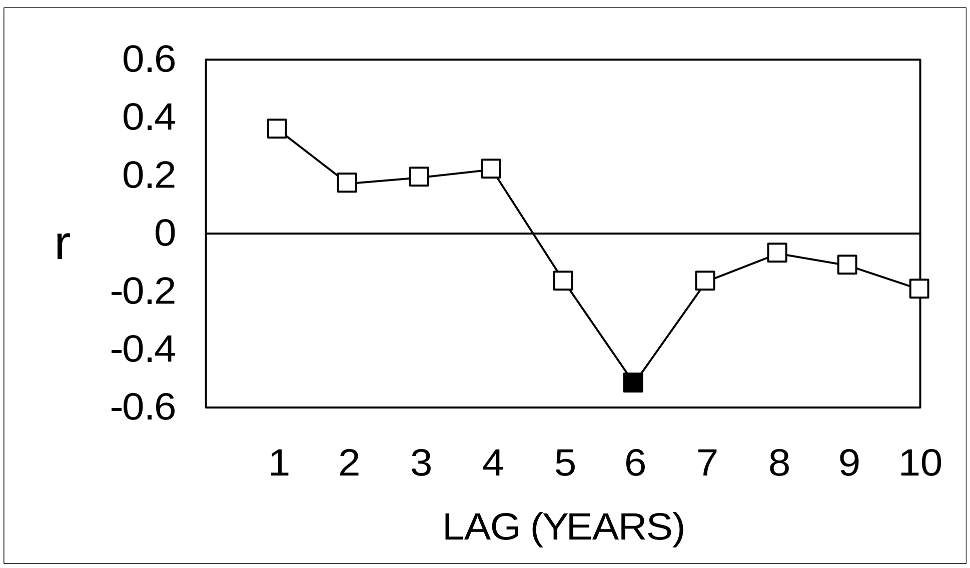

45
46
47
Breeding Bird Survey route
Breeding Ground Survey transect
Stratum boundary
PDSI reporting region


PONDS (X 1,000)
PDSI
r = 0.75
1000
800
600
400
200
0
6
5
4
3
2
1
0
-1
-2
-3
-4
-5
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004

(A)


0.6
0.4
0.2
0
-0.2
-0.4
-0.6
r
1 2 3 4 5 6 7 8 9 10
LAG (YEARS)

(B)


0.6
0.4
0.2
0
-0.2
-0.4
-0.6
r
1 2 3 4 5 6 7 8 9 10
LAG (YEARS)

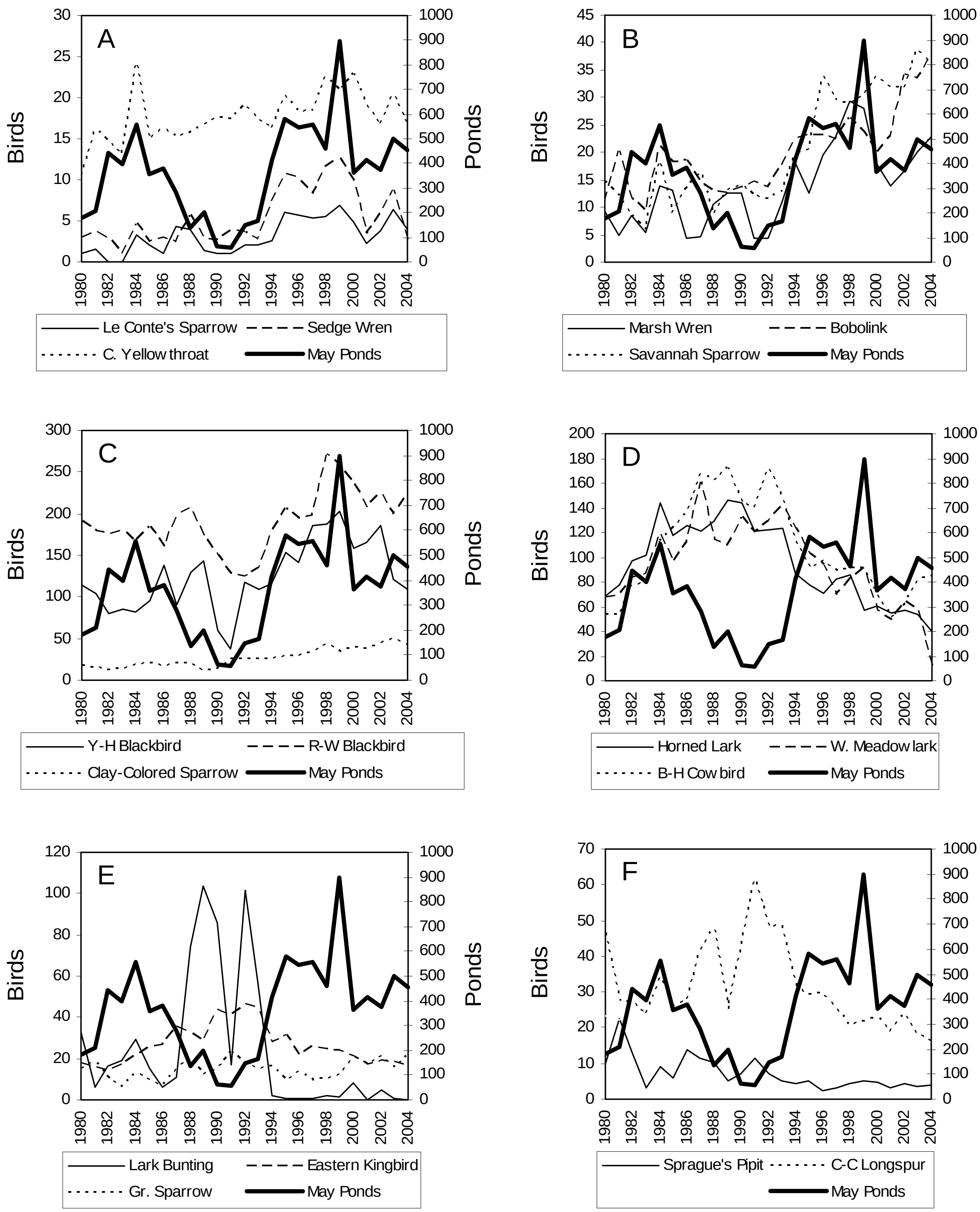

A
Birds
Ponds
Le Conte's Sparrow
Sedge Wren
C. Yellowthroat
May Ponds
B
Marsh Wren
Bobolink
Savannah Sparrow
May Ponds
C
Y-H Blackbird
R-W Blackbird
Clay-Colored Sparrow
May Ponds
D
Horned Lark
W. Meadowlark
B-H Cowbird
May Ponds
E
Lark Bunting
Eastern Kingbird
Gr. Sparrow
May Ponds
F
Sprague's Pipit
C-C Longspur
May Ponds

TABLE 1. Species included in analyses of associations between bird detections and moisture indices in northern North Dakota, 1980-2004; reported response 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 (S*turnella 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 et al. 2005b; 8: Fletcher and Koford (2004).

[b]Cody (1985) reported response to water from >1 time period.

TABLE 2. Mean, minimum, maximum, and ratio between minimum and maximum number of birds observed annually per BBS 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]
C-c 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]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.

TABLE 3. Akaike weights for null model and models assessing associations between mean number of birds detected on routes and two moisture indices and time periods in northern North Dakota, 1980-2004. Bold face indicates 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 percent of variation that was explained by moisture conditions in the model with the greatest Akaike weight.

Species	Null model	Ponds (current)	PDSI (current)	Ponds (current and previous years)	PDSI (current and previous years)	R^2
Eastern Kingbird	0.04	**0.45**	0.04	**0.45**	0.03	26.3
Horned Lark	0.02	**0.28**	0.25	**0.28**	0.17	28.0
Sedge Wren	0.00	**0.65**	0.02	0.31	0.02	44.3
Marsh Wren	0.00	**0.57**	0.00	0.42	0.00	43.2
Sprague's Pipit	0.15	**0.29**	0.18	0.16	0.22	14.8
Common Yellowthroat	0.14	**0.57**	0.11	0.14	0.03	19.6
Clay-colored Sparrow	0.11	**0.37**	0.15	0.29	0.08	17.9
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	45.0
Savannah Sparrow	0.01	0.32	0.02	**0.60**	0.05	37.8
Grasshopper Sparrow	0.15	**0.43**	0.25	0.11	0.06	17.1

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	41.3
C-c Longspur	0.00	**0.53**	0.04	0.42	0.01	46.4
Bobolink	0.05	**0.62**	0.12	0.18	0.03	26.4
Western Meadowlark	0.13	0.21	0.07	**0.56**	0.03	22.1
Red-winged Blackbird	0.00	0.03	0.00	**0.97**	0.00	54.8
Yellow-headed Blackbird	0.02	**0.57**	0.04	0.31	0.07	32.3
Brown-headed Cowbird	0.07	0.34	0.12	**0.37**	0.10	29.4
Mean	0.10	**0.38**	0.12	0.33	0.07	32.2

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

TABLE 4. Akaike weights for null model and models assessing association between percentage of routes on which birds were detected and two moisture indices and time periods in northern North Dakota, 1980-2004. Bold face indicates 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 percent of variation that was explained by moisture conditions in the model with the greatest Akaike weight.

Species	Null model	Ponds (current)	PDSI (current)	Ponds (current and previous years)	PDSI (current and previous years)	R^2
Sedge Wren	0.07	**0.56**	0.15	0.14	0.08	23.9
Marsh Wren	0.09	0.25	**0.40**	0.13	0.12	19.7
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	52.9
Savannah Sparrow	0.08	**0.32**	0.41	0.08	0.10	19.0
Grasshopper Sparrow	0.00	0.01	0.01	**0.63**	0.35	43.4
Baird's Sparrow	0.22	0.15	**0.38**	0.12	0.13	13.6
Le Conte's Sparrow	0.07	0.18	0.12	0.11	**0.52**	25.1
C-c Longspur	**0.53**	0.14	0.21	0.05	0.07	[a]
Mean	0.17	0.22	**0.26**	0.16	0.20	28.2

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

APPENDIX A. Sum of squares error (SSE) and AIC_c differences (Δ_i) for null model and models assessing associations between number of birds detected on routes and two moisture indices and time periods in northern North Dakota, 1980-2004. Number of parameters (K) was two for the null model, three for current-year models, and four for combined-year models. Sample size was 25 for all models.

	Null model		Ponds (current)		PDSI (current)		Ponds (current and previous years)		PDSI (current and previous years)	
Species	SSE	Δ_i	SSE	Δ_i	SSE	Δ_i	SSE	Δ_i	SSE	Δ_i
Eastern Kingbird	2,190	5.04	1,614	0.01	1,942	4.64	1,439	0.00	1,804	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	271.8	12.05	151.3	0.00	199	6.85	143	1.45	179.8	7.17
Marsh Wren	1,286	11.55	730.4	0.00	1,095	10.12	668	0.62	1,024	11.30
Sprague's Pipit	517.9	1.39	441.5	0.00	459.1	0.98	412.3	1.15	403.3	0.59
Common Yellowthroat	233.7	2.84	188	0.00	214.1	3.25	187.2	2.75	211.5	5.80
Clay-colored Sparrow	3,066	2.35	2,516	0.00	2,700	1.76	2,289	0.49	2,523	2.93
Vesper Sparrow	1,655	0.00	1,646	2.46	1,641	2.39	1,625	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	2,553	8.60	1,714	1.24	2,103	6.35	1,455	0.00	1,773	4.94
Grasshopper Sparrow	542	2.09	449.4	0.00	469.8	1.11	446.8	2.71	469.4	3.95
Baird's Sparrow	373.1	0.00	371.5	2.49	362.3	1.86	362.5	4.73	352.6	4.04
Le Conte's Sparrow	104.5	10.74	61.3	0.00	84.2	7.94	55.3	0.28	70	6.18
C-c Longspur	3,343	13.00	1,791	0.00	2,207	5.22	1,627	0.46	2,184	7.82
Bobolink	1,318	5.04	971	0.00	1,110	3.34	957	2.49	1,095	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 AIC_c differences (Δ_i) for null model and 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. Number of parameters (K) was 2 for the null model, 3 for current-year models, and 4 for combined-year models. Sample size was 25 for all models.

	Null model		Ponds (current)		PDSI (current)		Ponds (current and previous years)		PDSI (current and previous years)	
Species	SSE	Δ_i	SSE	Δ_i	SSE	Δ_i	SSE	Δ_i	SSE	Δ_i
Sedge Wren	7,066	4.24	5,376	0.00	5,971	2.62	5,357	2.77	5,613	3.94
Marsh Wren	7,680	2.90	6,400	0.94	6,165	0.00	6,031	2.31	6,041	2.35
Sprague's Pipit	2,874	0.00	2,724	1.26	2,870	2.56	2,620	3.14	2,633	3.27
Lark Bunting	13,609	16.24	7,393	3.58	6,406	0.00	6,698	3.97	5,919	0.88
Savannah Sparrow	1,890	3.16	1,531	0.49	1,501	0.00	1,531	3.35	1,494	2.74
Grasshopper Sparrow	4,579	10.95	3,630	7.74	3,819	9.01	2,376	0.00	2,491	1.18
Baird's Sparrow	5,492	1.06	5,102	1.81	4,745	0.00	4,639	2.29	4,619	2.18
Le Conte's Sparrow	14,116	3.93	11,840	2.13	12,224	2.93	10,947	3.03	9,697	0.00
C-c Longspur	2,732	0.00	2,731	2.59	2,653	1.86	2,633	4.53	2,591	4.13