POTENTIAL EFFECTS OF GLOBAL WARMING ON WATERFOWL POPULATIONS BREEDING IN THE NORTHERN GREAT PLAINS

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Abstract. The Prairie Pothole Region (PPR) of the Northern Great Plains is the most important breeding area for waterfowl in North America. Historically, the size of breeding duck populations in the PPR has been highly correlated with spring wetland conditions. We show that one indicator of climate conditions, the Palmer Drought Severity Index (PDSI), is strongly correlated with annual counts (from 1955 to 1996) of both May ponds ($R^2 = 0.72$, $p < 0.0001$) and breeding duck populations ($R^2 = 0.69$, $p < 0.0001$) in the Northcentral U.S., suggesting the utility of PDSI as an index for climatic factors important to wetlands and ducks. We then use this relationship to project future pond and duck numbers based on PDSI values generated from sensitivity analyses and two general circulation model (GCM) scenarios. We investigate the sensitivity of PDSI to fixed changes in temperature of 0°C, +1.5°C, +2.5°C, and +4.0°C in combination with fixed changes in precipitation of -10%, +0%, +7%, and +15%, changes spanning the range of typically-projected values for this region from human-induced climatic change. Most (11 of 12) increased temperature scenarios tested result in increased drought (due to greater evapotranspiration under warmer temperatures) and declining numbers of both wetlands and ducks. Assuming a doubling of CO_2 by 2060, both the equilibrium and transient GCM scenarios we use suggest a major increase in drought conditions. Under these scenarios, Northcentral U.S. breeding duck populations would fluctuate around means of 2.1 or 2.7 million ducks based on the two GCMs, respectively, instead of the present long-term mean of 5.0 million. May pond numbers would fluctuate around means of 0.6 or 0.8 million ponds instead of the present mean of 1.3 million. The results suggest that the ecologically and economically important PPR could be significantly damaged by climate changes typically projected. We make several recommendations for policy and research to help mitigate potential effects.

Keywords: effects of global warming, drought, climate change, Prairie Pothole Region, waterfowl breeding ecology, wetlands

Climatic Change **40**: 343–369, 1998.

1. Introduction

The Prairie Pothole Region (PPR) in the Northern Great Plains of North America is the most productive duck habitat in the world. Characterized by gently rolling hills and a high density of shallow wetlands, the potholes comprise only 10% of North American waterfowl breeding habitat, but produce 50-80% of the continent's ducks (Batt et al., 1989). The PPR also provides important habitat for migrating waterfowl that breed further north, as well as breeding and migration habitat for millions of other birds. Global climatic change is expected to alter many aspects of wetland hydrology, biogeochemistry and function (IPCC, 1996b; other papers in this volume). Of special concern to us is how anticipated changes in the hydrologic regimes of wetlands in the Northern Great Plains will affect populations of prairie-nesting waterfowl, birds that are dependent on shallow wetlands for breeding.

Natural variation in temperature and rainfall in the PPR causes both annual and seasonal variation in the distribution and number of wetlands during the breeding season. This in turn affects both the size of duck populations settling to breed in the area and their reproductive success. The importance of wetland habitat conditions (most often indexed by the number of ponds holding water in spring, i.e., May Ponds) to breeding duck population sizes and productivity has been documented in many studies (e.g., Krapu et al., 1983; Johnson and Grier, 1988). When suitable wetlands are unavailable in the PPR, as occurs during periodic drought, ducks may be displaced northward where productivity is lower, forego breeding completely or experience drastically reduced breeding success (Rogers, 1964; Pospahala, et al. 1974; Derksen and Eldridge, 1980; Cowardin et al., 1985). Therefore, in order to understand how waterfowl populations might be affected by climatic change, we need to understand how the wetlands on which they so strongly depend will be affected.

Assuming a doubling of CO_2 over its pre-industrial level, general circulation models (GCMs) for central North America generally project warmer and drier conditions in the Northern Great Plains (IPCC, 1990). This result holds for both equilibrium models (IPCC, 1990) and newer transient runs (IPCC, 1996a). Doubled CO_2 simulations consistently show temperature increases in the range of 2 to 5° C in winter and 1 to 4° C in summer in this region. There is less agreement regarding precipitation changes, but most models show an increase in precipitation in winter by 5 to 20% and no change or a decrease of up to 10% in summer. In most model calculations, summer soil moisture is also projected to decrease due to increased evapotranspiration (e.g., Wetherald and Manabe, 1995). Both hydrological theory and climate models suggest that with no net change in precipitation or even a modest increase, drought frequency and severity are likely to increase due to the much greater atmospheric demand for water that will occur with projected increases in temperature (Hansen et al., 1989; McCabe et al., 1990; Rind et al., 1990; Rosenzweig and Hillel, 1993). Because of enhanced evapotranspiration, wet years are likely to be wetter than in the past and dry years drier, and thus an increase in hydrologic extremes is anticipated (IPCC, 1996a). Droughts of the late 1980's and recent flooding in this region perhaps herald this predicted increase in climatic variability.

Two studies modeling the effects of predicted climatic change on prairie wetlands suggest that both the number and quality of prairie wetlands will decrease in a warmer, drier climate (Poiani and Johnson, 1991; 1993; Larson, 1995). In addition, prairie wetlands were much more sensitive to changes in temperature than to changes in precipitation for the range of values tested.

The objective of this paper is to assess the potential impact of climatic change on both wetland numbers and duck population size in the PPR. Our assessment is possible because of the unrivaled historical data base for North American duck populations and wetland habitat conditions maintained by the U.S. Fish and Wildlife Service's Office of Migratory Bird Management. Systematic aerial surveys provide robust annual estimates (1955 - present) of waterfowl population size and wetland abundance across 1.3 million square miles of important breeding habitat in the Northcentral U.S., parts of Canada, and Alaska. First, we examine whether a drought index - the Palmer Drought Severity Index (PDSI) - is a good predictor of the number of wetlands and number of ducks counted during annual surveys, and could therefore serve as an index of habitat conditions and predictor of future duck populations. We then use sensitivity simulations and projections of the PDSI from two different GCMs to assess the future likelihood of drought and its effects on wetland and duck numbers.

We define the PPR to include Southcentral Prairie Canada (southern half of Manitoba, Saskatchewan and Alberta) and the Northcentral U.S. (North Dakota, South Dakota, and eastern Montana). Because Canadian climate data have proven much more difficult to obtain than U.S. data, we report here results for only the Northcentral U.S. Analyses for Prairie Canada will be presented in a subsequent paper.

2. Methods

2.1. WATERFOWL AND WETLANDS SURVEY DATA

We used data from nine survey strata (41-49) in the Northcentral U.S. from the May Breeding Waterfowl and Habitat Surveys conducted annually by the United States Fish and Wildlife Service (Fig. 1, Henny et al., 1972). Counts of

TABLE I

Fourteen most abundant duck species counted each May and July in the Breeding Waterfowl and Habitat Surveys conducted annually by the U.S. Fish and Wildlife Service. Species are listed in order of decreasing abundance in survey strata 41-49 in the Northcentral U.S.

Common name	Scientific name
Blue-winged teal	*Anas discors*
Mallard	*Anas platyrhynchos*
Northern pintail	*Anas acuta*
Gadwall	*Anas strepera*
Northern shoveler	*Anas clypeata*
Redhead	*Aythya americana*
American wigeon	*Anas americana*
Lesser scaup	*Aythya affinis*
Ruddy duck	*Oxyura jamaicensus*
Green-winged teal	*Anas crecca*
Canvasback	*Aythya valisineria*
Ring-necked duck	*Aythya collaris*
Bufflehead	*Bucephala albeola*
Common goldeneye	*Bucephala clangula*

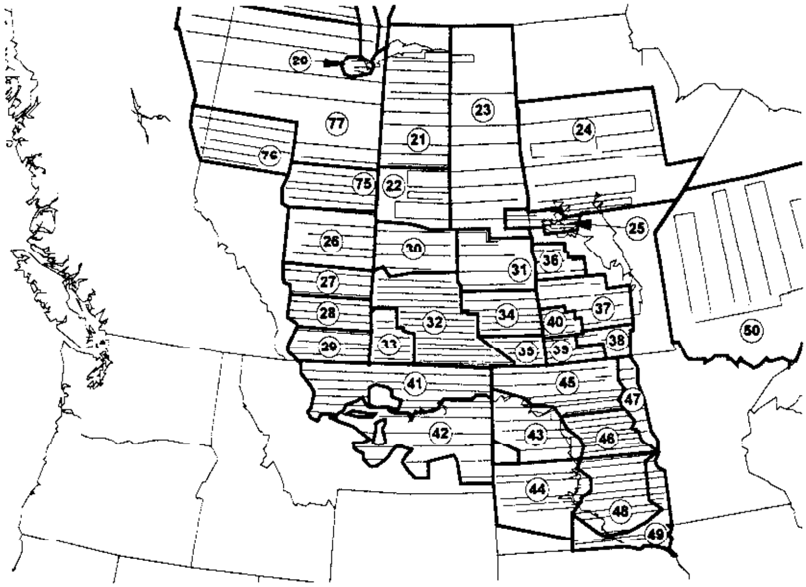

Figure 1. Transects and strata for areas of the Breeding Waterfowl and Habitat Survey.

ducks and wetlands are made each May and July from aircraft flying at low altitude along linear transects within each stratum (Smith, 1995). All identifiable ducks and pond basins containing water that occur within 200 m on one side of the transect are counted. Wetlands that are flooded seasonally, semi-permanently and permanently are included in the count (Shaw and Fredine, 1956); temporary wetlands (holding water for only a few weeks) and sheetwater are not counted. Air-Ground Comparison Surveys are conducted on a subsample of aerial transect routes throughout the PPR to provide annual visibility correction factors for both wetlands and ducks (Smith, 1995). We used forty-two years of survey data (1955-1996) for duck population estimates. We summed counts for the 14 most abundant species (Table I) breeding in this region to estimate the total duck breeding population size each year. Annual variation in these numbers primarily reflects changes in breeding duck settling patterns in relation to local habitat conditions rather than major shifts in overall population size. Although pond counts were begun in the 1960s, we used pond count data only from 1974 to the present, years when a visibility correction factor was in effect for all strata. The number of ponds counted in May is the only index of annual wetland conditions readily available on a large scale for use in waterfowl population studies (e.g., Pospahala et al., 1974; Batt et al., 1989; Caithamer and Dubovsky, 1996).

2.2. CLIMATE DATA

Much of the annual variation in the number of wetland basins holding water can be explained by climatic factors. For example, Larson (1995) found empirically that 63% of the variation in the percentage of basins holding water in grassland regions could be explained by a combination of precipitation (total for the year, and amount during fall of the previous year) and temperature variables (fall mean maximum, and difference between mean minimum and mean maximum in April), and the number of wet basins counted the previous May. To project future conditions, we were interested in identifying a single composite measure of dryness or wetness that used climate variables simulated by GCMs. We assessed whether the PDSI could serve as this index by examining the relationships between 1) wetland numbers and PDSI, and 2) duck numbers and PDSI.

The PDSI translates observed monthly temperature and precipitation into a hydrological water budget (Palmer, 1965). The index reflects the balance between moisture supply and demand, taking into account precipitation and stored soil moisture (supply), potential evapotranspiration, water storage, and runoff (demand), as well as previous conditions (i.e., wetness in one month is related to the previous month). The measurements are normalized so that comparisons of the index can be made among locations and time periods.

The PDSI is commonly used in a variety of applications, including the monitoring of soil moisture conditions for agricultural purposes and as a drought-monitoring tool (see for example, USDA's Weekly Crop Bulletin). The index varies roughly from -6.0 to +6.0 with higher values indicating wetter than normal weather and lower values indicating drought conditions (Table II). The PDSI may provide a more reliable indication of future drought conditions than other measures (e.g., soil-moisture change by GCMs), because it utilizes a more realistic calculation of potential evapotranspiration (Rind et al., 1990).

We obtained May PDSI values from the National Climatic Data Center's (NCDC) archive of monthly weather data (available at ftp://ftp.ncdc.noaa.gov) for the 22 climate divisions (1955-1996) overlaying the nine U.S. Fish and Wildlife survey strata in the Northcentral U.S. Values for May of each year were averaged over the 22 divisions. Associations between these values and those of both wetland numbers and total duck numbers in the region were tested using simple linear regression. An examination of the residuals from these initial analyses revealed the presence of positive autocorrelation in the observations, typical of time series data. Years of similar PDSI, pond numbers or duck numbers tended to follow each other, therefore violating the assumption of independent errors required for regression analysis. We confirmed the presence of autocorrelated error with the Durbin-Watson test and then re-estimated the regression equations using the Cochrane-Orcutt procedure (Neter at al., 1990). This procedure removes the autocorrelation by transforming the variables with an autocorrelation parameter, rho. Ordinary least squares regression is then used with the transformed variables to yield the

TABLE II

Palmer Drought Severity Index (PDSI) Classifications for Dry and Wet Periods

PDSI	Class
4.00 or more	Extremely wet
3.00 to 3.99	Very wet
2.00 to 2.99	Moderately wet
1.00 to 1.99	Slightly wet
0.50 to 0.99	Incipient wet spell
0.49 to -0.49	Near normal
-0.50 to -0.99	Incipient dry spell
-1.00 to -1.99	Mild drought
-2.00 to -2.99	Moderate drought
-3.00 to -3.99	Severe drought
-4.00 or less	Extreme drought

fitted regression model and more accurate parameter estimates. All analyses were performed using SPSS (version 6.1.1 with Trends module) for the Macintosh.

2.3. SENSITIVITY SIMULATIONS AND GCM CLIMATE CHANGE

GCMs are in general agreement in their projection of increased temperature assuming a doubling of CO_2 (although the magnitude of warming varies, particularly by region). Projections for rainfall, however, vary among models and are considered less certain. We therefore first performed sensitivity simulations of PDSI using various combinations of fixed temperature and precipitation changes that covered the range of values typically projected by climate models for the region. Such sensitivity analyses are useful for identifying a range of plausible scenarios for the forecast variable (PDSI) and for assessing the differential responses of the duck-wetland system to this variable (e.g., Lamb, 1987; Schneider et al., 1992).

To take advantage of the regional and temporal specificity of GCM forecasts, we then used two GCM-based scenarios for future climate in the Northern Great Plains to project future PDSI values. We recognize, however, that climate modelers place lower confidence in regional GCM projections because of the limitations of current models to resolve the climate processes occurring at finer spatial scales needed for regional estimates (Grotch and MacCracken, 1991).

2.3.1. *PDSI Base Scenario*

We first calculated monthly PDSI values for the "base scenario" or current climate (1955-1996) of the Northern Great Plains. This allows comparisons of climate-change PDSI values (from the sensitivity simulations and GCM scenarios) with values from the "normal" climate of the base period (from 1955-1996) on a monthly basis. PDSI values were calculated using a program provided by the NCDC (Asheville, NC). Observed monthly mean temperature and precipitation for the 22 Northcentral U.S. climate divisions (1955-1996) were obtained from the NCDC's archive of monthly weather data and averaged over the 22 divisions. The soil water capacity and latitude, needed as inputs to the PDSI program, were also averaged over the 22 divisions. Potential evapotranspiration (PET), a key component in analysis of the PDSI, was calculated using the Thornthwaite (1948) method. A detailed description of the PDSI water budget method is provided in Palmer (1965).

The calibration period used for the PDSI calculations was the same period for which waterfowl data were available, 1955-1996. The PDSI values we derived for the base period (1955-1996) were highly correlated with the archival values published by NCDC (correlation coefficients ranged from

0.93 - 0.95); small differences were probably due to the different calibration periods used (NCDC uses 1931-1990).

2.3.2. *PDSI Sensitivity Simulations*

The PDSI program computes wetness/dryness with respect to normal conditions at a given site. The mean base PDSI is close to zero if the calibration period is the same as the period of interest. In order to use the PDSI program for climate change impact studies, the calculated base coefficients for the calibration period that define "normal" wetness/dryness of a region are usually held constant (e.g., Rind et al., 1990), as was done in this study.

For the sensitivity simulations, combinations of temperature increases of 0°C, +1.5°C, +2.5°C, and +4.0°C and precipitation changes of -10%, 0%, +7%, and +15% were applied uniformly to all months during the period 1955-1996. These changes span the range of estimates from most state-of-the-art GCM scenarios. Although uniform changes across seasons are unrealistic, determining the sensitivity of PDSI to a variety of average temperature and precipitation changes is useful nonetheless for evaluating possible transient climatic responses, assessing which climate variables have the most affect on PDSI, and providing a range of potential outcomes. Because the PDSI is based on the Thornthwaite formulation for potential evapotranspiration, the responses to temperature may be overestimated.

2.3.3. *GCMs*

The projections produced by two GCMs for future climate change were also used in the PDSI program to assess the effects of potential future climate on soil-water conditions. Two different types of GCM scenarios were used. The first was an 'equilibrium simulation' where atmospheric CO_2 is doubled all at once and held fixed while the model climate is allowed to approach a new equilibrium. The second was a 'transient simulation' in which CO_2 was gradually increased through time (1%/year increase in equivalent CO_2). Both types of simulations assume that CO_2 values will have doubled from pre-industrial values by about the year 2060. Both types of simulations also produce a control (1 x CO_2) scenario which is a simulation of the current climate. The equilibrium and transient GCMs used in this study were those of the Geophysical Fluid Dynamics Laboratory (GFDL-QFlux model; Manabe and Wetherald, 1987) and United Kingdom Hadley Center (UKHC; Murphy and Mitchell, 1995), respectively. The two GCM scenarios are based on recent simulations with a range of climate sensitivity (globally averaged annual projections for the GFDL-QFlux model - temperature +2.5° C, precipitation +12.8%; UKHC (transient) model - 2020s +2.2° C, precipitation +3.8%, 2050s +3.3° C, precipitation +6.4%).

Average monthly differences in temperature and ratios of precipitation were obtained for both GCMs by comparing the changed CO_2 level simulation run with the control simulation run. Monthly changes (April - August) in temperature and precipitation predicted to occur in the Northcentral U.S. for these conditions are shown in Tables III and IV, respectively. For doubled or near-doubled CO_2 conditions, increases in monthly temperature ranged from about 3.5 to 6.6° C for the equilibrium model and 2.6 to 6.8° C for the transient model. An increase of ~1.0° C is projected for May of the 2020s and about 2.9 for May of the 2050s by the UKHC transient GCM, while increases close to 3.5° C are projected for May of 2060 by the GFDL equilibrium GCM. Early spring flooding followed by decreased precipitation in late spring and summer months is predicted by the GFDL equilibrium scenario (Table IV), although most decreases are small. Increases in precipitation are projected for most months by the UKHC scenario (2020s and 2050s), with the largest increases in May. These model-predicted changes in temperature (differences) and precipitation (ratios) were applied to the observed monthly temperature and precipitation data to generate the PDSI values for the 2 x CO_2 climate change scenarios. The GCM-predicted climate changes were obtained by interpolating between GCM

TABLE III

Current (1 x CO_2) and projected surface air temperature values (°C) and their difference for the Northcentral U.S. (April August) for the GFDL equilibrium doubled CO_2 climate change scenario and UKHC transient climate change scenario (2020s and 2050s).

Month	1 x CO_2	Projected temperature (°C)	Difference
GFDL (2 x CO_2)			
April	6.8	10.4	3.6
May	12.1	15.6	3.5
June	17.5	22.3	4.8
July	23.7	30.3	6.6
August	26.5	31.3	4.8
UKHC 2020s			
April	3.9	4.9	1.0
May	10.1	11.1	1.0
June	15.4	17.5	2.1
July	18.8	23.7	4.9
August	20.0	25.1	5.1
UKHC 2050s			
April	3.9	6.5	2.6
May	10.1	13.0	2.9
June	15.4	17.9	2.5
July	18.8	23.5	4.7
August	20.0	26.8	6.8

grid-boxes (as opposed to using the nearest grid-box) to the mean latitude and longitude of the study area.

TABLE IV

Current (1 x CO_2) and projected precipitation values (mm/day) and their ratio for the Northcentral U.S. (April - August) for the GFDL equilibrium doubled CO_2 climate change scenario and UKHC transient climate change scenario (2020s and 2050s).

Month	1 x CO_2	Projected precipitation (mm/day)	Ratio
GFDL (2 x CO_2)			
April	1.3	2.5	1.9
May	2.4	2.1	.9
June	3.1	3.0	1.0
July	2.1	1.4	.7
August	1.0	1.0	1.0
UKHC 2020s			
April	1.4	1.8	1.3
May	2.0	2.7	1.4
June	3.6	3.7	1.0
July	3.5	3.8	1.1
August	3.3	2.3	.7
UKHC 2050s			
April	1.4	1.9	1.4
May	2.0	3.1	1.6
June	3.6	3.7	1.0
July	3.5	3.6	1.0
August	3.3	2.1	.6

3. Results

3.1. REGRESSION OF PONDS AND DUCKS ON THE PDSI

For the Northcentral U.S. from 1974 to 1996, we found a strong positive relationship between the observed total number of May ponds each year and the corresponding year's average May PDSI ($R^2 = 0.72$, $p < 0.0001$, Figure 2a). May PDSI values were strongly negative during the well-known drought years of 1977, 1980 and 1988 when pond numbers were correspondingly low (Figure 2b). PDSI values for 1995 and 1996 stand out as much wetter than normal and May pond counts for the Northcentral U.S. were at record high levels.

The relationship between average May PDSI and size of the total duck population settling to breed in the Northcentral U.S. from 1955 to 1996 is also significantly positive ($R^2 = 0.69$, $P < 0.0001$, Figure 3a). During the drought years of the late 1950s, 1977, 1980, and the late 1980s, both PDSI values and duck numbers were at their lowest (Figure 3b). Peaks in population

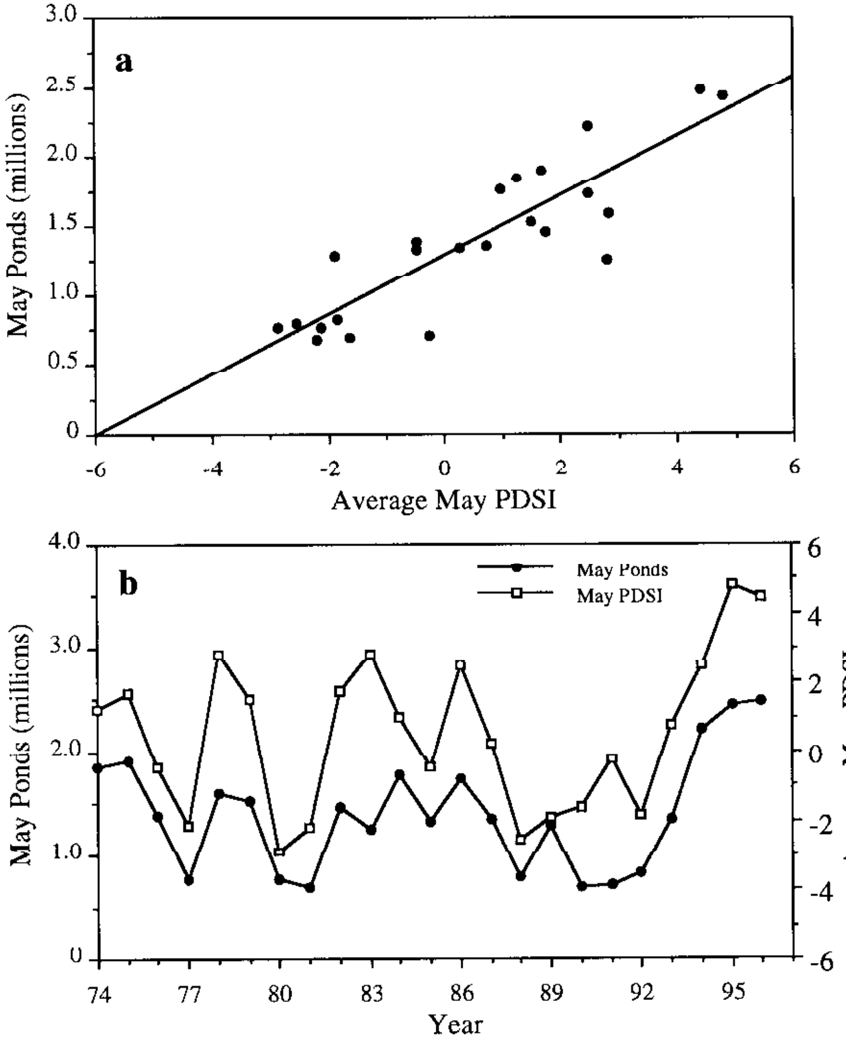

Figure 2. Number of May ponds and average May PDSI values for the Northcentral U.S., 1974 - 1996, graphed as a scatter plot (a) and as a time series (b). Regression model: May ponds = 1,283,368 + 200,944(average May PDSI). Regression coefficients were estimated using the Cochrane-Orcutt procedure for time series with first-order autocorrelated errors (autocorrelation coefficient rho = 0.22).

size coincide with more positive May PDSI values, which indicate years with wetter than normal conditions. With extremely wet conditions in 1995 and 1996, the size of the breeding population reached record highs, highlighting the overwhelming importance of wetland conditions for breeding waterfowl.

Based on the strong positive relationships between these variables, we suggest that the number of May ponds and the size of duck breeding

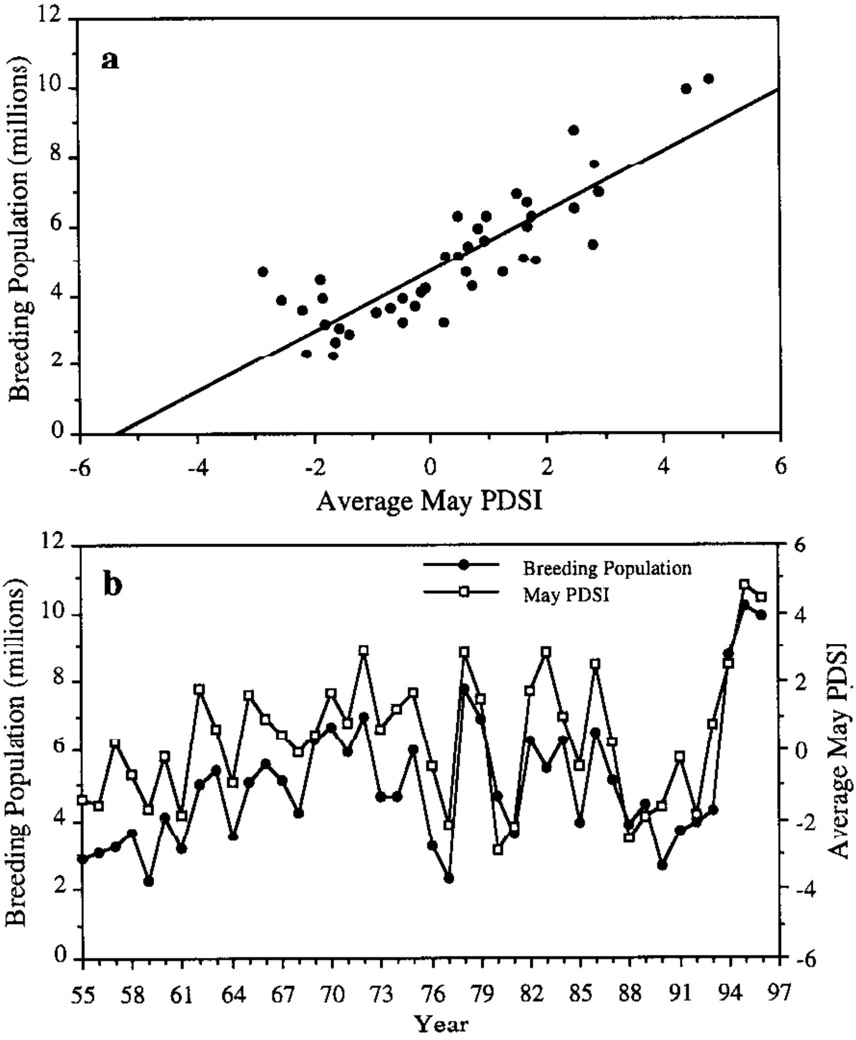

Figure 3. May breeding duck population estimates and average May PDSI values for the Northcentral U.S., 1955 -1996, graphed as a scatter plot (a) and as a time series (b). Regression model: breeding population size = 4,787,536 + 796,159(average May PDSI). Regression coefficients were estimated using the Cochrane-Orcutt procedure for time series with first-order autocorrelated errors (autocorrelation coefficient rho = 0.31).

populations can be credibly projected into the future based on projections of the PDSI.

3.2. SENSITIVITY SIMULATIONS

PDSI values for the base period (1955-1996 observations) and those derived from sensitivity simulations (15 different combinations of temperature and precipitation changes) for 5 spring and summer months (April - August) are provided in Table V. Projected PDSI values can be compared with the long-term mean May PDSI for this region of 0.37 (NCDC data) and a mean of -0.01 when 1955-1996 is the calibration period.

TABLE V

Palmer Drought Severity Index values for the Northcentral U.S. (April - August) for the base period (1955-1996) and for 15 sensitivity simulations. All sensitivity simulations were done by applying an annual uniform change in temperature and/or precipitation to base values for each month.

Experiment	April	May	June	July	August
Base (1955-1996)	-.09	-.01	.02	-.16	-.07
+1.5°C	-2.43	-2.42	-2.59	-2.83	-2.78
+2.5°C	-4.06	-4.26	-4.44	-4.79	-5.04
+4.0°C	-6.22	-6.60	-7.04	-7.54	-7.88
+7% precip.	1.37	1.36	1.50	1.59	1.84
+7% precip., +1.5°C	-.83	-.85	-.85	-1.10	-1.01
+7% precip., +2.5°C	-2.67	-2.68	-2.79	-3.03	-2.99
+7% precip., +4.0°C	-5.06	-5.36	-5.55	-5.97	-6.30
+15% precip.	3.12	3.22	3.51	3.81	4.06
+15% precip., +1.5°C	.54	.53	.74	.73	.79
+15% precip., +2.5°C	-.88	-.92	-.88	-1.11	-1.00
+15% precip., +4.0°C	-3.67	-3.79	-3.94	-4.22	-4.28
-10% precip.	-2.23	-2.16	-2.35	-2.56	-2.51
-10% precip., +1.5°C	-4.36	-4.58	-4.84	-5.23	-5.53
-10% precip., +2.5°C	-5.71	-6.04	-6.48	-6.97	-7.31
-10% precip., +4.0°C	-7.70	-8.19	-8.81	-9.42	-9.83

PDSI values are highly sensitive to changes in temperature. A +1.5° C increase in temperature alone results in average PDSI values of -2 to -3, which corresponds to "moderate drought" as the average condition. This result is due mostly to increased evapotranspiration brought on by higher temperatures. Similarly, +2.5° C and +4.0° C increases with no change in precipitation result in PDSI values less than -4 (extreme drought).

The increases in precipitation we tested generally do not fully compensate for deficits in the water budget that arise from increased evapotranspiration with warmer temperatures, a result reported for many other studies (e.g., Gleick, 1987; McCabe et al., 1990; Poiani et al., 1995). A 7% increase in precipitation did not offset the effect of even the lowest temperature increment, +1.5° C. A 15% increase in precipitation would compensate for a +1.5° C increase in temperature, but would not offset a +2.5° C increase in temperature. By extrapolation, an approximately 30% increase in precipitation would be needed to offset a temperature increase of +4.0° C.

3.3. GENERAL CIRCULATION MODEL SCENARIOS

Under the GFDL climate change scenario, the average predicted 2 x CO_2 May PDSI for this region produced by the PDSI model was -3.40; severe drought would be the average condition (Table VI). The mean May PDSI predicted for the 2020s under the UKHC transient model was -1.41 (mild drought) and for the 2050s was -2.59 (moderate drought). PDSI values become increasingly negative into the summer months in both models. The drier conditions projected by the GFDL model compared to the UKHC model are not unexpected given the temperature and precipitation changes projected by this model (Tables III and IV).

TABLE VI

Projected values of the Palmer Drought Severity Index for the Northcentral U.S. (April - August) from the GFDL equilibrium doubled CO_2 climate change scenario and UKHC transient climate change scenario (2020s and 2050s).

Climate scenario	April	May	June	July	August
GFDL (2 x CO_2)	-2.42	-3.40	-4.16	-5.64	-6.36
UKHC 2020s	-2.23	-1.41	-1.83	-2.26	-3.70
UKHC 2050s	-3.75	-2.59	-2.89	-3.36	-5.16

3.4. PROJECTIONS OF WETLAND AND DUCK ABUNDANCE

Using the regression models from section 3.1 and projections of PDSI for this region, the number of May ponds and size of the duck breeding population can be projected into the future and compared with present long-term means (Table VII).

With an average May PDSI of -3.40 (severe drought) projected for this region by the equilibrium GFDL model, May pond numbers are projected to fluctuate around a mean of 0.6 million, 54% less than the long-term mean. Total breeding duck population size in the Northcentral U.S. is predicted to fluctuate around a mean of 2.1 million, 58% less than the long-term mean. These projected averages are slightly lower than the lowest annual values recorded from 1955 to 1996 (Figures 2b and 3b).

With mild drought (PDSI -1.41) predicted to be the average condition in the 2020s by the UKHC transient model, May pond numbers are projected to fluctuate around a mean of 1.0 million, 23% less than the long-term mean and total duck population size is projected to be 3.7 million, 26% less than the long-term mean. Similarly, an average May PDSI of -2.59 (moderate drought) forecast for the 2050s yields May pond and duck numbers that fluctuate around means of 0.8 million (38% decrease) and 2.7 million (46% decrease), respectively.

Projections of May pond numbers and duck breeding population size based on projected May PDSI values from the sensitivity simulations are shown in Figures 4a and 4b, respectively. Both May pond numbers and duck population size decrease from long-term means for 11 of the 12 simulations with temperature increases. Decreases would be relatively small for +1.5° C/+7% precipitation and +2.5° C/+15% precipitation simulations: projected number of May ponds for both of these scenarios was about 1.1 million (15% decrease from the long-term mean). Projected breeding population size for both scenarios was 4.1 million (18% decrease). Simulations combining no change or decreased precipitation with temperature increases result in large to catastrophic reductions in May pond numbers and duck population size. In +1.5° C and +2.5° C scenarios with no change in precipitation, May pond numbers decrease 39% and 67%, respectively; duck population sizes decrease

TABLE VII

Current averages for May PDSI, May ponds and size of the duck breeding population (1955 - 1996) and projections for these variables from the GFDL equilibrium doubled CO_2 climate change scenario and UKHC transient climate change scenario (2020s and 2050s). Values for May pond numbers and size of the breeding population for the GCM scenarios are projected from the historical relationships between May pond numbers and May PDSI, and size of the breeding population and May PDSI, respectively (see Figures 2 and 3).

Scenario	May PDSI	May Pond Numbers (millions)	Size of Breeding Population (millions)
1955 - 1996*	0.37	1.3	5.0
GFDL (2 x $C0_2$)	-3.40	0.6	2.1
UKHC 2020s	-1.41	1.0	3.7
UKHC 2050s	-2.59	0.8	2.7

* Values for May PDSI and size of the breeding population are 42 year averages for 1955 - 1996 (PDSI data from NCDC archive); May pond numbers is the average for 1974 - 1996.

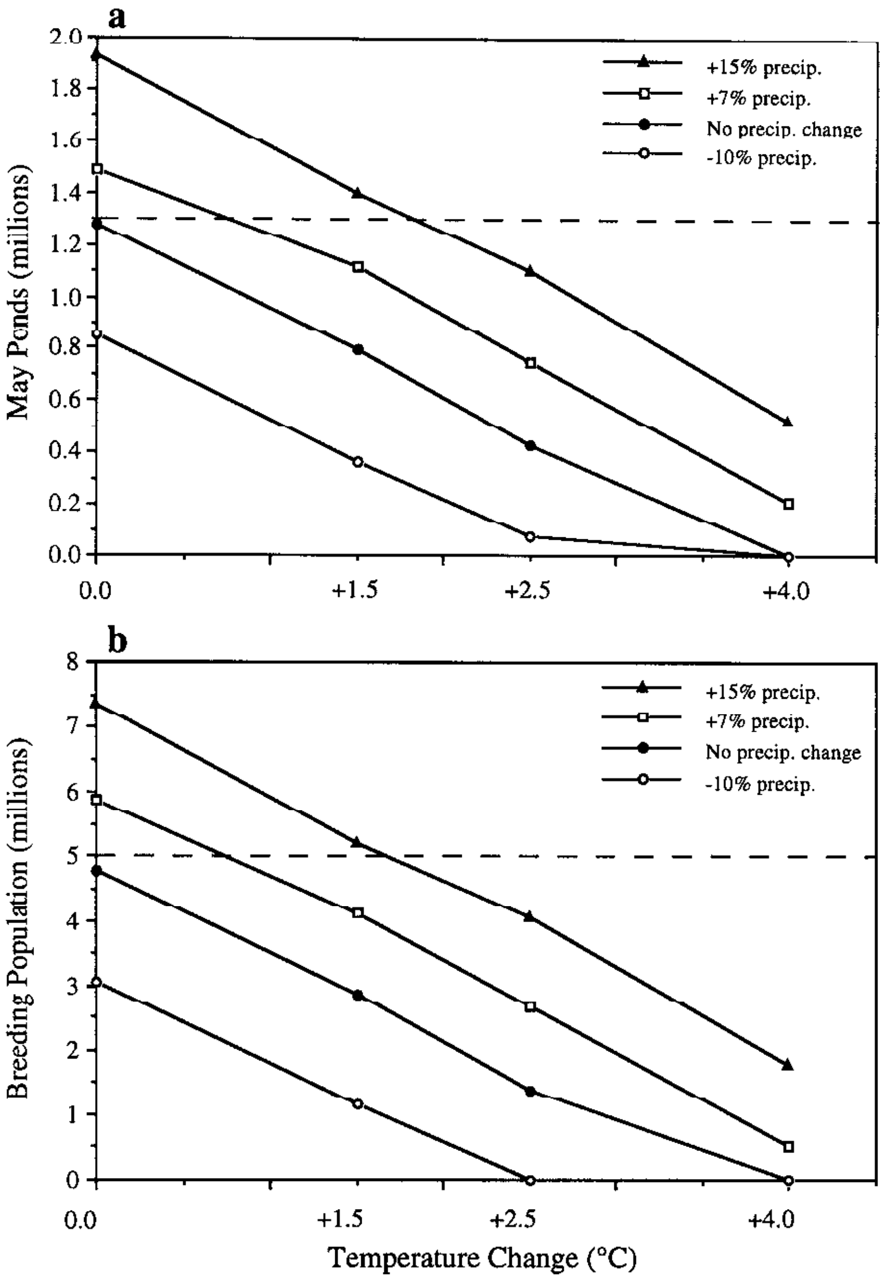

Figure 4. Projected number of May ponds (a) and projected duck breeding population sizes (b) for the base period and for 15 sensitivity simulations. Values were calculated using May PDSI values from Table III and the regression model equations for May ponds and breeding population size in Figures 2 and 3, respectively. Dashed lines show long-term (1955-1996) means.

43% and 72%, respectively. May pond numbers and duck numbers both increase in simulations combining precipitation increases with no change in temperature, but these scenarios are unlikely, given the ever-increasing accumulation of greenhouse gases in the atmosphere and mounting evidence on the effects of these gases on climate (IPCC 1996a).

4. Discussion

Our analyses of historical data show that May PDSI is an excellent predictor of both the number of wetlands and the size of duck populations settling to breed in the Northcentral U.S. Projections of PDSI for the Northcentral U.S. from sensitivity simulations and two GCMs suggest that, even with a modest increase in precipitation, conditions will become much drier in this region due to increased evapotranspiration caused by warmer temperatures. If current climate models prove to be approximately valid and the projected temperature increases lead to increased droughtiness as reflected by lower average PDSI values, then the number of wetlands, and consequently the number of ducks, in this region is likely to decline drastically in the coming decades.

Unlike the situation for most species, we already know a great deal about how waterfowl are affected by climate (Johnson, 1992). Field studies show that drought, in addition to affecting population settling patterns, also affects waterfowl nesting in at least six ways: 1) Increased frequency of non-breeding (during severe drought, a large proportion of female ducks forego breeding completely (Bellrose, 1980; Krapu et al. 1983)); 2) Reduced clutch sizes (Davies and Cooke, 1983; Krapu et al., 1983); 3) Shortened breeding season (Dzubin and Gollup, 1972; Krapu et al., 1983); 4) Reduced frequency of renesting (during drought, many females will attempt to nest only once rather than attempting 2, 3, 4, and even 5 nests during wet years following losses to predators (Bellrose, 1980; Krapu et al. 1983; Cowardin et al., 1985)); 5) Lower nest success due to less nesting cover and shifts in food habits of predators (Cowardin et al., 1985; Greenwood et al., 1995); 6) Lower brood survival, possibly due to a) poorer food resources or higher predation associated with longer overland moves by ducklings to find food and water (Ball et al., 1975; Rotella and Ratti, 1992a), or, b) less available flooded cover. In order for populations to be maintained, recruitment rate must compensate for annual mortality (i.e., the number of young that enter the breeding population must equal the number of adults that die). All of the above effects lead to lowered recruitment rates, and assuming constant mortality rates, declining population sizes.

The great climatic variability of the PPR produces a "boom or bust" system in which highly productive waterfowl habitat occurs in only about 3 years in 10 (Baldassare and Bolen 1994). Waterfowl have evolved to survive these conditions, and historically have been able to maintain their numbers and recover from periodic drought. Prolonged drought in the 1980s, however, combined with ongoing wetland drainage and destruction of upland nesting habitat for agriculture led to the lowest duck numbers ever recorded in the late 1980s. A return of good water conditions in combination with nesting habitat enhancement programs, especially the Conservation Reserve Program, has led to the recent recovery of most species. Modeling research suggests that with climate change, the frequency of extreme weather events may increase, making a run of drought or flood years more likely (Mearns et al., 1984, IPCC 1996a). If the frequency as well as the severity of drought increases, the sustainability of waterfowl populations is in question. Likewise, a greater likelihood of successive wet years (like 1993-1997) could be highly conducive to population growth. The trend projected by climate models, however, is clearly towards drying, suggesting that the overall affect of climate change on waterfowl population size and reproduction is likely to be negative.

We should also emphasize that the positive relationship between May PDSI and duck numbers that we have shown here, as well as the historical relationship between May pond numbers and duck population size, primarily reflects variation in settling patterns of breeding birds in relation to local habitat conditions, rather than dramatic annual fluctuations in the overall North American populations of these species. During wet years on the prairies when many wetland basins are flooded, migrating pairs are attracted to the area as they fly north from their wintering grounds in South America, Mexico, or the southern U.S., and a large proportion of the North American population settles there to breed (Johnson and Grier, 1988; Batt et al., 1989). During drought years, however, many ducks over-fly the prairie potholes and move northward into parkland, boreal forest and tundra habitats (Johnson and Grier, 1988). What happens to birds that move on to these other areas becomes a key question, the answer to which may be different in the future than it is now. Birds displaced northward by prairie drought are thought to have lower productivity which results in declines of the continental duck population after several successive drought years on the prairies (Hansen and McKnight, 1964; Crissey, 1969; Calverly and Boag, 1977). Nevertheless, the more stable northern habitats support sizable breeding populations and serve as an important habitat for drought-displaced prairie ducks. We do not know if northern regions will provide suitable breeding habitat in a changed climate. The hydrologic regimes of these wetlands will also be altered, but the extent of the alteration is not known. For example, warmer temperatures are likely to cause a melting of permafrost that may lead to lowered water tables and drying of northern wetlands (Gorham, 1994; Mimikou et al., 1991; IPCC 1996b). In addition, Larson (1995) showed that the more northern parkland wetlands within the PPR may be more sensitive to changes in temperature than prairie wetlands. Thus, the potential for ducks to find suitable alternative breeding areas in a drier future may be limited.

Our predictions of declining population sizes in the U.S. PPR are based on the assumption that ducks will continue to settle in response to wetland abundance (i.e. the number of ducks per pond will remain relatively constant over a range of pond numbers), and that as habitat availability decreases, birds will not settle at appreciably higher densities. The present diversity in size and type of wetlands in the PPR, as well as the great number of ponds, provide ideal habitat for breeding (Swanson, 1988; Krapu and Duebbert, 1989). These wetland complexes provide isolation for breeding pairs, thereby minimizing competition for food resources (particularly aquatic invertebrates, crucial sources of protein needed by breeding females) and reducing sexual harassment of breeding females by paired and unpaired males (McKinney et al., 1983). Many studies also show the importance of wetland complexes to duckling survival (e.g., Talent et al., 1983; Rotella and Ratti, 1992a, b). If there is widespread reduction in wetland availability, ducks may, over time, crowd together in less desirable habitat. Birds will likely adapt to increasing pair density up to some point, but negative effects on survival and reproduction are likely. Studies of waterfowl breeding in crowded urban environments and wintering in overcrowded refuges reveal a higher frequency of disease, aggression, and sexual harassment (Friend, 1981; McKinney et al., 1983).

Our projection of fewer wetlands in an anthropogenically-warmed climate is consistent with the findings of two wetland modeling studies. Larson's (1995) models projected that a 3° C increase in temperature would result in 22% and 56% declines in the number of wet basins in grassland and parkland habitats, respectively (parklands in the northern portion of the PPR have wetlands surrounded by aspen and willow trees). Simulations of a single, semi-permanent wetland conducted by Poiani and Johnson (1993) showed earlier-than-normal drying of the wetland each year, and water level fluctuations around a lower mean level. Wetland quality (measured by value as duck breeding habitat) is also likely to decline in a warmer climate. Poiani and Johnson (1993) also showed that a balanced (50:50) ratio between emergent vegetation and open water (the ratio favored by ducks, Kaminski and Weller, 1992; Murkin et al., 1997), shifted dramatically towards a wetland completely closed by vegetation.

In our sensitivity simulations, prairie wetlands were more sensitive to changes in temperature than to changes in precipitation over the range of values tested, a result also reported by Larson (1995) and Poiani and Johnson (1993). Most (11 of 12) increased temperature scenarios we investigated resulted in increased drying (more negative PDSI) and declining numbers of both ponds and ducks. Large increases in precipitation (15%) would be required to offset the negative effects on PDSI of even a small temperature increase (+1.5° C).

One limitation of our PDSI sensitivity simulations is application of uniform changes in temperature and precipitation to all months of the year. Temperature increases and changes in precipitation are expected to vary seasonally (IPCC, 1996a). Although projections for precipitation are especially variable and uncertain, many models for Central North America predict an increase in winter precipitation and no change or a decrease in summer rainfall (IPCC, 1996a). This scenario could result in early spring flooding from greater snow melt run-off and earlier drying of wetlands in summer. Breeding waterfowl are attracted to flooded wetland conditions and may, over time, respond to warmer temperatures and earlier wetland availability by shifting their migration and breeding schedules to earlier in the season, as has been shown for a number of other species (e.g., Beebee, 1995; Crick et al., 1997). Excessive spring flooding, however, can reduce available nesting cover and result in nesting delays, especially for diving duck species that nest in emergent vegetation. If wetlands dry too early in summer, renesting effort, nest success, brood survival, and other components of reproductive success would likely be adversely affected (see above). A potential net result of these conditions is that the PPR might act as a population sink area, i.e., the region attracts breeding pairs but produces too few young to compensate for annual mortality.

Poiani et al. (1995) investigated the potential effects of increased temperature combined with seasonally-varying changes in precipitation on the hydrology of a semi-permanent wetland. Most of their seasonal scenarios (including scenarios with increased precipitation) resulted in lower water levels compared to the current climate due to greater evapotranspiration under higher temperatures. Increased spring precipitation (which included snow melt runoff) was the only scenario in which water level in the wetland did not decline below the level of the current climate. Because of the importance of winter snow melt for recharging prairie potholes (Winter, 1989), this scenario of relatively greater winter precipitation presents a better prognosis for waterfowl than any other seasonal pattern. This range of possible responses highlights the critical need for GCMs with greater accuracy at the regional level, as well as a better understanding of how seasonal changes in temperature and precipitation will affect wetland habitat. Also in need of study is how anticipated changes in the variability and frequency of extreme events (e.g., droughts, floods, Mearns et al., 1984; IPCC 1996a) will affect wetland habitat and waterfowl population dynamics.

It also will be important to consider impacts on wetlands and waterfowl from changing agricultural practices. Aside from periodic drought, the principle cause of low recruitment in duck populations is the cumulative loss and degradation of wetlands and upland nesting cover caused by expansion of cultivation (Patterson, 1995). Over the past 100 years most of the native grasslands in the PPR have been converted to croplands that are tilled annually (Cowardin et al., 1983). Nest success in landscapes dominated by spring-seeded croplands is notoriously low (e.g., Greenwood et al., 1995). On Conservation Reserve Program lands in the U.S. (cropland that has been converted to perennial cover), there is recent evidence that nest survival is positively correlated with the proportion of perennial grass cover on four square-mile study plots (R. Reynolds, pers. comm.). Any future conversion of annual cropland to grassland would likely benefit waterfowl nest success although this advantage would be diminished by water scarcity. Most studies simulating the effects of climate change on agriculture in the Central Plains show potential for reduced yields of major field crops (not surprising if drought increases) and potential for agricultural expansion northward (Rosenzweig 1985; Rosenberg, 1992; Rosenzweig and Hillel, 1993). It seems likely that climate-induced reductions in yield and cropland expansion, coupled with human population growth and increased demand for grain in the next century, will make it increasingly difficult to set aside productive agricultural land for conservation.

4.1. RECOMMENDATIONS FOR POLICY AND FUTURE RESEARCH

Based on our current insights, we have some recommendations for conservation organizations, managers and policy makers to help mitigate some probable effects of global warming on waterfowl in the PPR. These include:

1. Gathering of better baseline data on the numbers, productivity and habitat relationships of birds breeding outside the primary survey areas in the PPR. This will help us to detect long-term trends in habitat conditions and the responses of waterfowl to those changed conditions (e.g., settling rates, recruitment rates). This knowledge is essential to enable intelligent responses to changes.

2. More sophisticated annual monitoring of habitat conditions in the PPR and other wetland regions important to waterfowl that are likely to be impacted by climate change. An improved understanding of waterfowl responses (e.g., settling, reproductive effort, nest survival, duckling survival) to wetland characteristics that are currently not measured (e.g., permanence, distribution, vegetation) and land use (e.g., perennial vegetation) would enable us to better assess potential effects of climate change.

3. Current conservation investments, particularly for long-term securement, should be targeted to less drought-prone portions of the PPR.

Wetland areas likely to be impacted by expanding agriculture should also receive attention now before they are extensively drained or altered.

4. More protections should be provided for wetlands, such as enhancing long-term legal securement of water for managed wetlands where possible. Preservation of existing wetlands through policy initiatives such as the Conservation Reserve Program and Wetlands Reserve Program in the U.S. should be continued and expanded. This will allow society to a) retain options in the future under any climate change scenario, and b) respond appropriately to developments such as unanticipated geographic heterogeneity in drought severity. Moreover, it would reduce direct impacts on wetlands now that are likely only to compound the negative effects of global climate change.

5. Further study of the probable impacts of climatic change on waterfowl populations is warranted. It is likely that future wetland conditions will vary geographically (e.g., prairie vs. parkland wetlands) and that, depending on life history traits, species will differ in their responses to climatic change. We are therefore currently extending the present analysis to the Canadian PPR (approximately 80% of the PPR is in Canada) and are examining the historical relationship between PDSI and individual species of waterfowl. Additional field studies of duck responses (especially reproductive success) to drought conditions should also be conducted. The current wet period in the PPR will probably end soon. When drier conditions return, a rare opportunity will exist to study the response of large populations to diminished wetland availability because duck populations are presently near historical highs. Modeling studies should explore the implications of more "pulsed" recruitment, likely in a more strongly fluctuating breeding environment, for the dynamics of exploited populations of ducks.

6. An important general recommendation for conservationists is simply to prepare for change. If nothing else is certain, we can be confident that the environment for wildlife in the PPR will change markedly during the next century. Conservation forces should remain vigilant, flexible and opportunistic. We need to anticipate changes that are coming, have the monitoring tools in place to detect important ecological patterns, act to counter changes that are highly likely to occur, and be ready to respond to significant but unpredictable events.

5. Conclusions

There is virtually no debate that continued increases of CO_2 will cause warming in all areas of the globe (IPCC 1996a). Climatologists are also highly confident that climatic change will have its greatest effect on wetlands by altering their hydrologic regimes (IPCC, 1995b). What remains uncertain in climate models (due to feedback mechanisms such as cloud cover, increased primary productivity, absorption of heat by the oceans, etc.) is the timing and geographic distribution of potential effects, particularly with regard to precipitation change (Schneider, 1989; Karl et al., 1997). Despite these uncertainties, our "best guess" from state-of-the-art climate models is that drought will become more frequent and severe during the next century in the northern Great Plains. Our analyses, together with those of Larson (1995) and Poiani and Johnson (1991; 1993) suggest that the wetland ecosystem of the Prairie Pothole Region is extremely sensitive and vulnerable to these projected climate changes and that the consequences for waterfowl populations likely will be profound.

As we face unprecedented human-induced changes in global climate, we need to foresee potential impacts on the ecosystems that directly support the quality of life for humans and other living organisms. Such knowledge will allow us to better devise management plans and adaptation and mitigation strategies that will anticipate coming changes (e.g., Riebsame 1990). Analyses addressing potential impacts of climatic change on agriculture, water resources, forestry, energy, and a few other areas are under way (e.g., IPCC, 1996b), but potential effects on wildlife have largely been ignored to date (Root, 1997; but see La Roe, 1991; Johnston and Schmitz, 1997). We encourage more studies addressing the potential impact of climate change on other wildlife dependent on PPR wetlands as breeding and migration habitat, particularly those examining potential effects on the dynamics of food chains, as disturbance at one trophic level (e.g., invertebrate fauna) will likely have ramifications for the entire prairie wetland ecosystem.

We have shown that quantitative predictions about the effects of climate change are possible for at least one group of species, waterfowl. If the projected scenarios of warming for this region come to pass, the number of ducks settling to breed in this region is likely to decline dramatically and the reproductive output of those breeding will be much lower than it is today. Declining waterfowl numbers would mean not only serious ecological consequences for prairie ecosystems and the loss of an important source of aesthetic enjoyment for millions of North Americans, but also substantial economic losses. Expenditures associated with migratory waterfowl hunting in the U.S. totaled more than 630 million dollars in 1990 and increased to over one billion dollars in 1995 and 1996 (U.S. Department of the Interior, 1997; Hinkle, 1996), dollars that are an important source of revenue for conservation and local economies. Given the potentially serious consequences of global warming for waterfowl populations suggested by our analysis, as well as likely negative effects on other wildlife dependent on prairie wetlands, society has yet another urgent reason to act to slow greenhouse warming and safeguard the future of these resources.

Acknowledgments

We thank E. K. Hartig, C. Rosenzweig, S. H. Schneider, M. D. Sorenson and two anonymous reviewers for comments that greatly improved the manuscript. We are also grateful to E. Rothman (Univ. of Mich. Statistical Consultation and Research) for statistical advice, and M. Barney and S. Radke for help with the literature review. We wish to express our sincere appreciation to L. Pitelka for his encouragement and to Electric Power Research Institute for the grant to T.L. Root and L.G. Sorenson to support this work.

References

Baldassarre, G. A. and Bolen, E. G.: 1994, *Waterfowl Ecology and Management.* John Wiley and Sons, Inc., New York.

Ball, I. J., Gilmer, D. S., Cowardin, L. M. and Riechmann, J. H.: 1975, 'Survival of Wood Duck and Mallard Broods in North-Central Minnesota', *J. Wildl. Manage.* **39**, 776-780.

Batt, B. D. J., Anderson, M. G., Anderson, C. D. and Caswell, F. D.: 1989, 'The Use of Prairie Potholes by North American Ducks', in van der Valk, A.G. (ed.), *Northern Prairie Wetlands*, Iowa State University Press, Ames, pp. 204-227.

Beebee, T. J. C.: 1995, 'Amphibian Breeding and Climate', *Nature* **374**, 219-220.

Bellrose, F. C.: 1980, *Ducks, Geese, and Swans of North America*, Stackpole Books, Harrisburg, PA.

Caithamer, D. F. and Dubovsky, J. A.: 1996, 'Waterfowl Population Status, 1996', U.S. Fish and Wildlife Service, Office of Migratory Bird Management, Branch of Surveys and Assessment, 28 pp.

Calverley, B. K. and Boag, D. A.: 1977, 'Reproductive Potential in Parkland and Arctic-Nesting Populations of Mallards and Pintails (Anatidae)', *Can. J. Zool.* **55**, 1242-1251.

Cowardin, L. M., Gilmer, D. S. and Shaiffer, C. W.: 1985, 'Mallard Recruitment in the Agricultural Environment of North Dakota', *Wildl. Monogr.* **92**, 1-37.

Crick, H. Q. P., Dudley, C., Glue, D. E., and Thomson, D. L.: 1997, 'UK Birds Are Laying Eggs Earlier', *Nature* **388**, 526.

Crissey, W. F.: 1969, 'Prairie Potholes from a Continental Viewpoint', in Saskatoon Wetlands Seminar, *Can. Wildl. Serv. Rep. Ser.* **6**, pp. 161-171.

Davies, J. C. and Cooke, F.: 1983. 'Annual Nesting Productivity in Snow Geese: Prairie Droughts and Arctic Springs', *J. Wildl. Manage.* **47**, 291-296.

Derksen, D. V. and Eldridge, W. D.: 1980, 'Drought-displacement of Pintails to the Arctic Coastal Plain, Alaska', *J. Wildl. Manage.* **44**, 224-229.

Duebbert, H. F. and Frank, A. M.: 1984, 'Value of Prairie Wetlands to Duck Broods', *Wildl. Soc. Bull.* **12**, 27-34.

Dzubin, A. and Gollop, J. B.: 1972, 'Aspects of Mallard Breeding Ecology in Canadian Parkland and Grassland', *U.S. Fish and Wildl. Serv. Wildl. Res. Rep.* **2**, 113-152.

Friend, M.: 1981, 'Waterfowl Management and Disease: Independent or Cause and Effect Relationships?', *Trans. North Am. Wildl. Nat. Resour. Conf.* **46**, 94-103.

Gleick, P. H.: 1987, 'Regional Hydrologic Consequences of Increases in Atmospheric CO_2 and other Trace Gases', *Clim. Change* **10**, 137-161.

Gorham, E.: 1994, 'The Future of Research in Canadian Peatlands: a Brief Survey with Particular Reference to Global Change', *Wetlands* **14**, 206-215.

Greenwood, R. J., Sargeant, A. B., Johnson, D. H., Cowardin, L. M. and Shaffer, T. L.: 1995, 'Factors Associated with Duck Nest Success in the Prairie Pothole Region of Canada', *Wildl. Monogr.* **128**, 1-57.

Grotch, S. L. and MacCracken, M. C.: 1991 'The Use of General Circulation Models to Predict Regional Climatic Change', *J. of Climate* 4, 286 303.

Hansen, H. A. and McKnight, D. E.: 1964, 'Emigration of Drought-displaced Ducks to the Arctic', *Trans. North Am. Wildl. Nat. Resourc. Conf.* **29**, 119-126.

Hansen, J. I., Rind, D., Delgenio, A., Lacis, A., Lebedeff, S., Prather, M., Ruedy, R., and Karl, T.: 1989, 'Regional Greenhouse Climate Effects', in Proc. 2nd Amer. Conf. on Preparing for Climate Change, Climate Inst., Washington, D.C., pp. 211-229.

Henny, C. J., Anderson, D. R. and Pospahala, R. D.: 1972, 'Aerial Surveys of Waterfowl Production in North America, 1955-1971', *U.S. Fish and Wildl. Serv. Spec. Sci. Rep. Wildl.* **160**.

Hinkle, M. K.: 1996, *Oases for Wildlife, Small and Farmed Wetlands.* National Audubon Society, Washington, D.C.

Intergovernmental Panel on Climate Change.: 1990, 'Climate Change: The IPCC Scientific Assessment', Houghton, J. T. , Jenkins, G. J., and Ephraums, J. J. (eds). Cambridge University Press, Cambridge.

Intergovernmental Panel on Climate Change.: 1996a, 'Climate Change 1995 The Science of Climate Change', Houghton, J. T., Meira Filho, L. G., Callander, B. A., Harris, N., Kattenberg, A., and Maskell, K. (eds), Cambridge University Press, Cambridge.

Intergovernmental Panel on Climate Change.: 1996b, 'Climate Change 1995 Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses', Watson, R. T., Zinyowera, M. C., Moss, R. H. (eds). Cambridge University Press, Cambridge.

Johnson, D. H. and Grier, J. W.: 1988, 'Determinants of Breeding Distributions of Ducks', *Wildl. Monogr.* **100**, 1-37.

Johnson, D. H., Nichols, J. D. and Schartz, M. D.: 1992, 'Population Dynamics of Breeding Waterfowl' in Batt, B. D. J. et al. (eds), *Ecology and Management of Breeding Waterfowl*, University of Minnesota Press, Minneapolis, pp. 446-485.

Johnston, K. M. and Schmitz, M. D.: 1997, 'Wildlife and Climate Change: Assessing the Sensitivity of Selected Species to Simulated Doubling of Atmospheric CO_2 ', *Glob. Change Biol.* **3**, 531-544.

Kaminski, R. M. and Weller, M. W.: 1992, 'Breeding Habitats of Nearctic Waterfowl' in Batt, B. D. J. et al. (eds), *Ecology and Management of Breeding Waterfowl*, University of Minnesota Press, Minneapolis, pp. 568-589.

Karl, T. R., Nicholls, N. and Gregory, J.: 1997, 'The Coming Climate', *Sci. Am.* **276**, 78-83.

Krapu, G. L. and Duebbert, H. F.: 1989, 'Prairie Wetlands: Characteristics, Importance to Waterfowl, and Status' in Sharitz, R. R. and Gibbons, J. W. (eds), *Freshwater Wetlands and Wildlife*, DOE Symposium Series No. 61, OSDOE Office of Scientific and Technical Information, Oak Ridge, TN, pp. 811-828.

Krapu, G. L., Klett, A. T. and Jorde, D. G.: 1983, 'The Effect of Variable Spring Water Conditions on Mallard Reproduction', *Auk* **100**, 689-698.

Lamb, P. J.: 1987, 'On the Development of Regional Climatic Scenarios for Policy-oriented Climate Impact Assessment', *Bull. Am. Meteorol. Soc.*, **68**, 1116-1123.

La Roe, T.: 1991, The Effects of Global Climate Change on Fish and Wildlife Resources', *Trans. North Am. Wildl. Nat. Resour. Conf.* **56**, 171-176.

Larson, D. L.: 1995, 'Effects of Climate on Numbers of Northern Prairie Wetlands', *Clim. Change* **30**, 169-180.

Manabe, S. and Wetherald, R. T.: 1987, 'Large-scale Changes of Soil Wetness Induced by an Increase in Atmospheric Carbon Dioxide', *J. Atmos. Science* **44**, 1211-1236.

McCabe, Jr. G. J., Wolock, D. M., Hay, L. E. and Ayers, M. A.: 1990, 'Effects of Climatic Change on the Thornthwaite Moisture Index', *Water Res.Bull.* **26**, 633-643.

McKinney, F., Derrickson, S. R. and Mineau, P.: 1983, 'Forced Copulation in Waterfowl', *Behaviour* **86**, 250-294.

Mearns, L. O., Katz, R. W. and Schneider, S. H.: 1984, 'Extreme High-temperature Events: Changes in their Probabilities with Changes in Mean Temperature', *J. Climate Appl. Meteor.* **23**, 1601-1613.

Mimikou, M., Kouvopoulos, Y., Cavadias, G. and Vayianos, N.: 1991, 'Regional Hydrological Effects of Climate Change', *J. Hydrology* **123**, 119-146.

Murkin, H. R., Murkin, E. J. and Ball, J. P.: 1997, 'Avian Habitat Selection and Prairie Wetland Dynamics: a 10-Year Experiment', *Ecol. Applic.* **7**, 1144-1159.

Murphy, J. M. and Mitchell, J. F. B.: 1995, 'Transient Response of the Hadley Centre Coupled Ocean-atmosphere to Increasing Carbon Dioxide', *J. Climate* **8**, 36-80.

Neter, J., Wasserman, W. and Kutner, M. H.: 1990, *Applied Linear Statistical Models, 3rd ed.* Irwin, Barr Ridge, IL.

Palmer, W. C.: 1965, 'Meteorological Drought', *U.S. Dep. of Commerce Res. Pap.* **45**, 1-58.

Patterson, J. H.: 1995, 'The North American Waterfowl Management Plan and Wetlands for the Americas Programmes: a Summary', *Ibis* **137**, S215-S218.

Poiani. K. A. and Johnson. C. W.: 1991. 'Global Warming and Prairie Wetlands', *BioScience* **41**, 611-618.

Poiani, K. A. and Johnson, C. W.: 1993, 'Potential Effects of Climate Change on a Semi-permanent Prairie Wetland', *Clim. Change* **24**, 213-232.

Poiani, K. A., Johnson, C. W. and Kittel, T. G. F.: 1995, 'Sensitivity of Prairie Wetland to Increased Temperature and Seasonal Precipitation Changes', *Water Res. Bull.* **31**, 283-294.

Pospahala, R. S., Anderson, D. R. and Henny, C. J.: 1974, 'Population Ecology of the Mallard II. Breeding Habitat Conditions, Size of the Breeding Populations, and Population Indices', *U.S. Fish and Wildl. Serv. Res. Publ.* **115**. 73 pp.

Riebsame, W. E.: 1990, 'Anthropogenic Climate Change and a New Paradigm of Natural Resource Planning', *Prof. Geogr.* **42**, 1-12.

Rind, D., Goldberg, R., Hansen, J., Rosenzweig, C. and Ruedy, R.: 1990, 'Potential Evapotranspiration and the Likelihood of Future Drought', *J. Geophys. Res.* **95**, 9983-10,004.

Rogers, J. P.: 1964, 'Effect of Drought on Reproduction of Lesser Scaup', *J. Wildl. Manage.* **28**, 213-222.

Root, T.: 1997, 'How to Approach Assessing Climate Impacts on Animals', in Hassol, S. J. and Katzenberger, J. (eds), *Elements of Change 1996*, Aspen Global Change Institute, Aspen, CO, pp. 203-206.

Rosenberg, N. J.: 1992, 'Adaptation of Agriculture to Climate Change', *Clim. Change* **21**, 385-405.

Rosenzweig, C.: 1985, 'Potential CO_2-induced Climate Effects on North American Wheat Producing Regions', *Clim. Change* **7**, 367-389.

Rosenzweig, C. and Hillel, D.: 1993, 'Plant and Environment Interactions', *J. Environ. Qual.* **22**, 9-22.

Rotella, J. J. and Ratti, J. T.: 1992a, 'Mallard Brood Survival and Wetland Habitat Conditions in Southwestern Manitoba', *J. Wildl. Manage.* **56**, 499-507.

Rotella, J. J. and Ratti, J. T.: 1992b, 'Mallard Brood Movements and Wetland Selection in Southwestern Manitoba', *J. Wildl. Manage.* **56**, 508-515.

Schneider, S. H.: 1989, 'The Greenhouse Effect: Science and Policy', *Science* **243**, 771-781.

Schneider, S. H., Mearns, L., and Gleick, P. H.: 1992, 'Climate-Change Scenarios for Impact Assessment' in Peters, R. L. and Lovejoy, T. E. (eds), *Global warming and Biological Diversity*, Yale University Press, New Haven, pp. 38-52.

Shaw, S. P. and Fredine, C. G.: 1956, 'Wetlands of the United States', *U.S. Fish and Wildl. Serv. Circ.* **39**. 67 pp.

Smith, G. W.: 1995, 'A Critical Review of the Aerial and Ground Surveys of Breeding Waterfowl in North America', *Biol. Sci. Rept.* **5**.

Swanson, G. A.: 1988. 'Aquatic Habitats of Breeding Waterfowl', in Hook, D. D. (ed). *Ecology and Management of Wetlands. vol. 1. Ecology of Wetlands*, Timber Press, Portland, OR, pp. 195-202.

Talent, L. G., Jarvis, R. L. and Krapu, G. L.: 1983, 'Survival of Mallard Broods in South-Central North Dakota', *Condor* **85**, 74-78.

Thornthwaite, C. W.: 1948, 'An Approach Toward a Rational Classification of Climate', *Geogr. Rev.* **38**, 55-94.

U.S. Department of the Interior, Fish and Wildlife Service and U.S. Department of Commerce, Bureau of the Census: 1997, '1996 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation', Washington, D.C.

Wetherald, R. T. and Manabe, S.: 1995, 'The Mechanisms of Summer Dryness Induced by Greenhouse Warming', *J. Climate* **8**, 3096-3108.

Winter, T. C.: 1989, 'Hydrologic Studies of Wetlands in the Northern Prairie' in van der Valk, A.G. (ed.), *Northern Prairie Wetlands*, Iowa State University Press, Ames, pp. 16-54.