Spring 2012

WETLAND HYDRODYNAMICS AND LONG-TERM USE OF SPRING MIGRATION AREAS BY LESSER SCAUP IN EASTERN SOUTH DAKOTA

Sharon N. Kahara
South Dakota State University, snk6@humboldt.edu

Steven R. Chipps
South Dakota State University, steven.chipps@sdstate.edu

Great Plains Research 22 (Spring 2012):69–78

WETLAND HYDRODYNAMICS AND LONG-TERM USE OF SPRING MIGRATION AREAS BY LESSER SCAUP IN EASTERN SOUTH DAKOTA

Sharon N. Kahara[1]

Department of Natural Resource Management
South Dakota State University
Brookings, SD 57007

and

Steven R. Chipps

U.S. Geological Survey
South Dakota Cooperative Fish and Wildlife Research Unit
South Dakota State University
Brookings, SD 57007
Steven.Chipps@sdstate.edu

ABSTRACT—Lesser scaup (*Aythya affinis* [Eyton]) populations remain below their long-term average despite improved habitat conditions along spring migration routes and at breeding grounds. Scaup are typically associated with large, semipermanent wetlands and exhibit regional preferences along migration routes. Identifying consistently used habitats for conservation and restoration is complicated by irregular wetland availability due to the dynamic climate. We modeled long-term wetland use by lesser scaup in eastern South Dakota based on surveys conducted during below-average (1987–1989) and above-average (1993–2002) water condition years. Wetland permanence, longitude, and physiographic region were all significant determinants of use ($P < 0.01$). Long-term use was best described by a quadratic equation including wetland surface area variability, an index of wetland hydrodynamics that is linked to productivity, biodiversity, and value to waterfowl. Contrary to previous findings, our study shows that over the long term, lesser scaup are more than twice as likely to use permanent wetlands as they are semipermanent wetlands. The northern region of South Dakota's Prairie Coteau, which holds the highest density of hydrologically dynamic permanent wetlands, should be considered an area of conservation concern for lesser scaup. The criteria we identified may be used to identify important lesser scaup habitats in other regions of the Prairie Pothole Region.

Key Words: lesser scaup, Prairie Coteau, Prairie Pothole Region, wetland hydrodynamics, wetland surface area

INTRODUCTION

North America's Prairie Pothole Region encompasses approximately 800,000 km^2 and is characterized by millions of wetland depressions. The Prairie Pothole Region provides multiple ecosystem services; however, since the 1780s it has suffered drastic wetland losses primarily to agricultural production (Dahl 1990). The heaviest losses occurred in the southeast portion of the region, with Iowa reportedly losing 99% of its wetlands. By comparison, South Dakota has fared marginally better, retaining 65% of its original wetlands (Dahl 1990). However, many of the remaining wetlands continue to undergo changes due to adjacent agricultural practices, resulting in drainage, increased sediment, nutrient, and chemical inputs (Neely and Baker 1989; Gleason and Euliss 1998). Identifying areas of conservation concern is a critical need, especially given the spatial scale of the region, distribution of wetland basins, variable climate, and projected habitat changes due to climate change (Euliss et al. 2004; Johnson et al. 2005; Millett et al. 2009; Johnson et al. 2010).

[1] Current address: Humboldt State University, Arcata, CA 95521, email: snk6@humboldt.edu

Manuscript received for review, August 2011; accepted for publication, January 2012.

The Prairie Pothole Region has long been recognized as an important breeding area for waterfowl and a critical staging ground for spring migrants. Overall, the region supports over 300 bird species (Prairie Pothole Joint Venture 2003). Lesser scaup (*Aythya affinis* [Eyton]), a species of diving duck whose populations have declined significantly since the 1970s (USFWS 2010), migrate through eastern South Dakota's Prairie Pothole Region in large numbers each spring. The combined greater and lesser scaup populations remain 16% below their long-term average (5.1 ± 0.05 million; USFWS 2010). Recent studies attribute lesser scaup declines to changes in spring migration and breeding habitat quality (Austin et al. 1999). Availability and quality of wetlands throughout the upper Midwest play an important role in lesser scaup body condition (Anteau and Afton 2004), which may influence subsequent breeding success. Declines in the 1970s and 1980s were initially attributed to poor water conditions in the Prairie Pothole Region, when precipitation fell below long-term averages leading to widespread drought and temporary loss of wetland habitat. However, their populations continued to decline in the 1990s, which was, on average, the second-wettest decade of the century (Garbrecht and Rossel 2002; Millet et al. 2009). During this period, wetlands increased in size and number across the Prairie Pothole Region, became less isolated and in some instances, may have merged forming larger, deeper ponds (Kahara et al. 2009). Increased wetland availability is generally associated with increased waterfowl production (USFWS 2010); therefore, the reasons for the decline remain unclear, and it is imperative that we identify important habitat areas for further investigation.

Numerous studies of lesser scaup associate them with large, semipermanent wetlands (Holland 1997; Lindeman and Clark 1999; Mockler 2004; Anteau 2006), while others have found higher densities on permanent wetlands (Kantrud and Stewart 1977). One study observed that lesser scaup relied heavily on permanent wetlands in dry years (Allen 1986). We sought to identify the most important wetlands to migrating lesser scaup based on long-term records, as most of the previous studies based their results on relatively brief observation periods. Studies based on less than 10 years of observation may be inadequate for determining priority areas for conservation, as wetlands in the Prairie Pothole Region often exhibit drastic hydrologic variability that influences depth, size, permanence, abundance, and even spatial distribution in response to the cyclical dry-wet climate (Tiner 2003; Kahara et al. 2009). Phases of these climate cycles usually persist for 10–20 years (Diaz 1986), influencing water chemistry, vegetation, and biota (Euliss et al. 2004).

The temporary disappearance of shallow temporary and seasonal wetlands during extended droughts limits the use of these wetland types by most waterfowl (Euliss et al. 1999). However, these are rarely used by diving ducks such as lesser scaup. In extreme droughts, temporary loss of semipermanent wetlands may occur, as was observed during a severe dry period between 1988 and 1993 at the Cottonwood Lake study area in North Dakota (LaBaugh et al. 1996).

Lesser scaup also exhibit regional preferences (Holland 1997; Anteau 2006). In eastern South Dakota, more scaup were observed on wetlands in the Missouri and Prairie Coteaus than other physiographic regions (Holland 1997; Mockler 2004). Identifying consistently used spring migration habitat in the variable landscape of the Prairie Pothole Region would help focus conservation efforts on maintaining habitat quality and food availability in those habitats (Anteau and Afton 2004).

We examined long-term records of lesser scaup habitat associations in eastern South Dakota as influenced by wetland size, hydrology, location, and areal variability over a period of 16 years during which both below-average and above-average water conditions were experienced (Winter and Rosenberry 1998). These variables were used to prioritize areas for migrating lesser scaup.

MATERIALS AND METHODS

Study Area

The study was conducted in eastern South Dakota's Prairie Pothole Region, which encompasses about 91,700 km^2 east of the Missouri River. Approximately 10% of South Dakota's Prairie Pothole Region is comprised of depressional wetlands, mainly freshwater marshes formed by glaciation events during the Pleistocene era (Flint 1971; Johnson and Higgins 1997). We assessed five major physiographic regions in eastern South Dakota (Fig. 1). Physiographic regions differ in climate, soil types, hydrology, elevation, and relative proportion of wetland classes (Johnson and Higgins 1997). Hydrological conditions vary with cyclical dry-wet climate events. Average annual precipitation data from 25 stations across the study area were obtained from the South Dakota State University Climate Data website (http://climate.sdstate.edu/climate_site/climate.htm). Average precipitation during the survey period (1987–2002) was 486 mm, with the driest period occurring

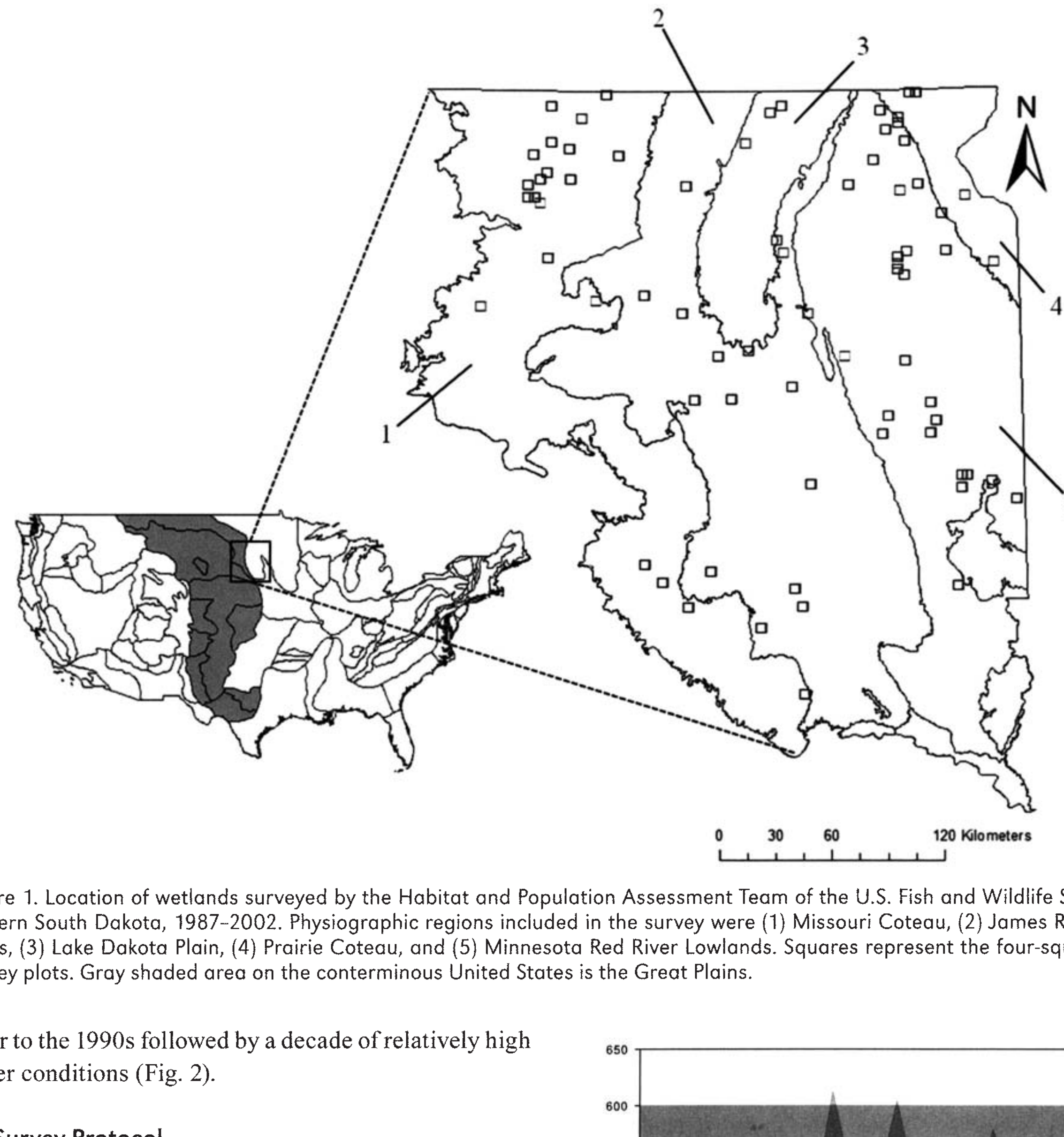

Figure 1. Location of wetlands surveyed by the Habitat and Population Assessment Team of the U.S. Fish and Wildlife Service in eastern South Dakota, 1987–2002. Physiographic regions included in the survey were (1) Missouri Coteau, (2) James River Lowlands, (3) Lake Dakota Plain, (4) Prairie Coteau, and (5) Minnesota Red River Lowlands. Squares represent the four-square-mile survey plots. Gray shaded area on the conterminous United States is the Great Plains.

prior to the 1990s followed by a decade of relatively high water conditions (Fig. 2).

Survey Protocol

We used survey data collected by the U.S. Fish and Wildlife Service Habitat and Population Assessment Team (USFWS-HAPET, Bismarck, ND) in eastern South Dakota from 1987 to 2002. During the survey period, 73 four-square-mile plots (approximately 10.4 km^2; Fig. 1) were randomly selected within five Fish and Wildlife Service Wetland Management Districts (Fig. 1). Over 17,000 surveys were conducted on 954 ponds from 1987 to 2002. Multiple ponds of varying hydrologic regime and size were selected within each four-square-mile plot. Surveys are conducted twice a year, the first from May 1 to May 15 and the second from May 20 to June 5. Observations of waterfowl and general wetland

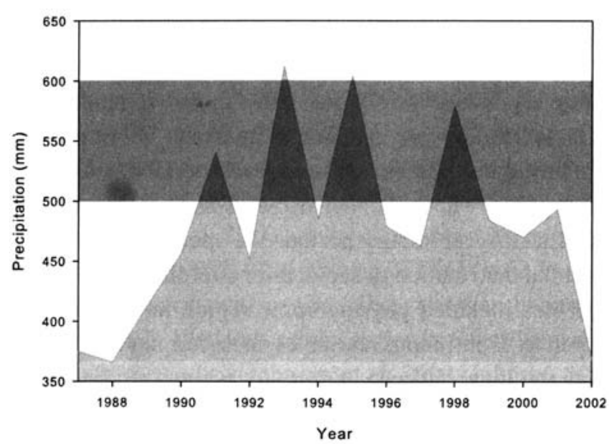

Figure 2. Average annual precipitation (mm) in eastern South Dakota (1987–2002), based on data from 25 weather stations (South Dakota Office of Climatology). Shaded area indicates annual average precipitation range based on data from 30-year climate normals, 1961–1990 (after Millet et al. 2009).

morphometry were made from vehicles using spotting scopes mounted on the window. Observers selected a set of vantage points from which they could view each wetland in its entirety, and recorded waterfowl numbers by species. General wetland morphometry (i.e., basin area, wet area, percentage of vegetation cover) was estimated in the field by surveyors. Surveys were conducted from morning to midafternoon, and time of day did not significantly influence numbers of birds observed (Mockler 2004). Surveyors classified wetlands into one of four categories based on water permanence following Stewart and Kantrud (1971), using the vegetative zone occupying the deepest or central part of the wetland basin to infer degree of water retention. These categories were (1) temporary, (2) seasonal, (3) semipermanent, and (4) permanent.

Statistical Analysis

Scaup Use vs. Non-use. We assessed scaup presence using a generalized linear mixed model specified for logistic distribution (SAS PROC GLIMMIX; SAS Institute 2004). Generalized linear mixed models are designed to perform estimation where data are nonparametric, autocorrelated, and nested. The model accounted for repeated measures over 16 years and overdispersion of the data. The response variable was scaup use vs. non-use; a binary variable. Continuous descriptive variables included wetland area, wetland wet area, and latitude and longitude. Class variables included survey period, wetland class, and physiographic region.

Long-Term Wetland Use. Long-term use of wetlands by lesser scaup was assessed using generalized linear mixed models. Our data included repeated measures made on multiple ponds within plots. Only those wetlands used by lesser scaup were included in analysis. We fit models explaining the number of years each pond was used by lesser scaup where number of years used was averaged over the 16-year survey period. We specified a negative binomial distribution to account for overdispersion. Class variables included physiographic region and water permanence. Continuous variables included survey period (May vs. June), latitude, longitude, average surface area, and wetland surface area variability. Wetland surface area variability was calculated as the difference between minimum and maximum surface area values for each wetland over the survey period. We modeled scaup use as a function of all possible combinations of the variables including interactions and quadratic effects.

Model fit was determined using a scaled Pearson's chi-square parameter. Pearson's chi-square is a goodness-of-fit measure that compares the predicted values of the outcome variable with the actual values where a value close to one was considered indicative of model adequacy (Pedan 2001). Models were then ranked using Akaike's Information Criterion (AIC), where AIC values were calculated from the negative log likelihood derived from each regression model (Burnham and Anderson 2002). Model weights (w_i) were then calculated as a measure of the support for each model. The relative importance of predictor variables was estimated by summing the AIC weights ($\sum w_i$) across the top 10 models in the candidate set where the variable occurred (Burnham and Anderson 2002).

We performed logistic regression (SAS PROC LOGISTIC) to specify the proportion of years each wetland was used by scaup. An odds ratio was calculated to provide an estimate of the relative likelihood of scaup using the Prairie Coteau compared to all other physiographic regions. Odds ratios compare odds of one event occurring relative to one specified response event (Equation 1). The value of the odds ratio may vary from 0 to infinity, with values equal to or around 1, indicating similar odds of both events occurring. We also estimated the odds of scaup using permanent wetlands compared to temporary, seasonal, and semipermanent wetland classes using a generalized linear mixed model procedure (SAS PROC GLIMMIX) specified for binary variables and repeated measures.

$$\textit{Odds ratio} = \left(\frac{p_i}{1-p_i}\right) \Big/ \left(\frac{p_j}{1-p_j}\right) \qquad \text{(Equation 1)}$$

where:

$\frac{p_i}{1-p_i}$ represents the odds of event i occurring, and

$\frac{p_j}{1-p_j}$ represents the odds of event j occurring.

We used the nearest neighbor interpolation tool in ArcGIS (version 9.3) to interpolate average change in wetland surface area, average years used by lesser scaup, and average number of lesser scaup counted over the survey period.

RESULTS

Average annual precipitation over the survey period included both below-average and above-average water conditions (Fig. 2) and was positively correlated with wetland area (Fig. 3; $r = 0.69$, $P < 0.01$). Average annual lesser scaup counts over the survey area were positively

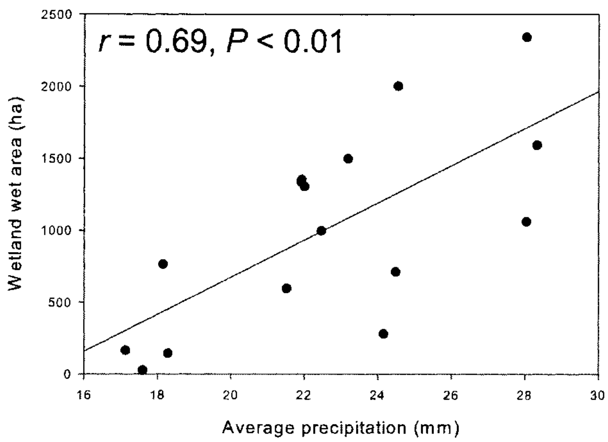

Figure 3. Average precipitation (mm) vs. average wetland wet area (ha) in eastern South Dakota, 1987–2002.

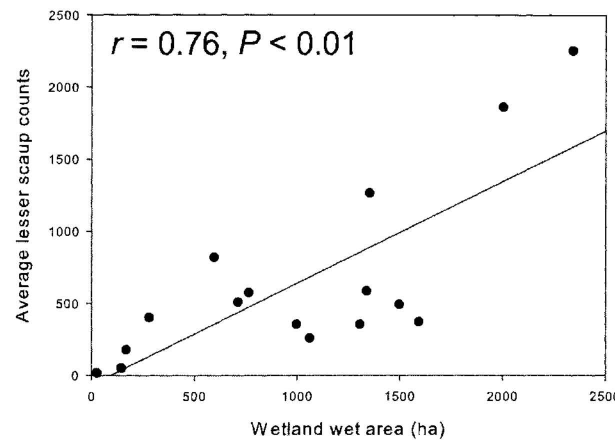

Figure 4. Average wetland wet area (ha) vs. average lesser scaup counts in eastern South Dakota, 1987–2002.

correlated with average wetland surface area (Fig. 4; $r = 0.73$, $P < 0.01$).

Scaup Use vs. Non-Use

Survey period ($P < 0.0001$), wetland class (water permanence) ($P < 0.01$), longitude ($P = 0.007$), and physiographic region ($P < 0.01$) were all significant determinants of scaup presence. Scaup presence, unlike scaup abundance, was not significantly related to wetland area ($P = 0.104$) or wetland wet area ($P = 0.479$). We found a significant difference between survey periods ($P < 0.01$), and so only data from the second survey was excluded from subsequent analysis. Furthermore, surveys conducted from May 1 to May 15 have been found to correspond best to peak scaup migration (Naugle et al. 2000; Austin et al. 2002; Mockler 2004).

Long-Term Wetland Use

The best-supported model explaining number of years a wetland was used by scaup included the quadratic term for change in surface area (Table 1). The next best model was physiographic region and wetland class, which had an ΔAIC of 9.1. Parameter estimates are given in Table 2. AIC weights indicated that the most important variable was wetland variability ($w_i = 0.99$), whereas physiographic region ($w_i = 0.01$) and average wetland area ($w_i = 0.001$) provided little explanatory value to the data (Table 3). Average change in wetland surface area ranged from 0 to 89 ha. The most variable wetlands were located in the Prairie Coteau physiographic region (Fig. 5A). The highest numbers of scaup and most frequently used areas were in the northern Prairie Coteau and northern Missouri Coteau (Figs. 5B and 5C).

The odds of migrating lesser scaup using the Prairie Coteau and Missouri Coteau were similar (Table 4). The odds of other physiographic regions being used by migrant scaup was less than half that of the Prairie Coteau. Semipermanent wetlands were only a third as likely to be used as permanent wetlands. Temporary wetlands were the least likely to be used by migrating scaup (Table 5).

CONCLUSIONS

Numerous studies have demonstrated the importance of spring migration habitat on waterfowl body condition, with implications for breeding success (e.g., Raveling and Heitmeyer 1989; Mainguy et al. 2002; Anteau and Afton 2004; Haukos et al. 2006). Drought conditions along migration routes and breeding grounds can influence migration chronology (Baar et al. 2008), force broods to move greater distances (Krapu et al. 2006), extend spring migration (Hupp et al. 2011), and reduce waterfowl carrying capacity (Smith 1971). The climate of the Prairie Pothole Region is semiarid, with considerable variations in rainfall (Winter 1989). Wetlands of the region are very sensitive to climate variability (Johnson et al. 2004; Johnson et al. 2005; Johnson et al. 2010). During severe droughts, many wetlands dry up completely, resulting in fewer available wetlands for waterfowl use and increased isolation among remaining basins (Shapley et al. 2005; Kahara et al. 2009).

Habitat conditions encountered along spring migration routes can impact body condition, timing of nesting,

TABLE 1
BEST-SUPPORTED MODELS BASED ON AKAIKE'S INFORMATION CRITERION VALUES OF FACTORS AFFECTING NUMBER OF YEARS USED BY LESSER SCAUP IN EASTERN SOUTH DAKOTA, 1987–2002

Variables	Scaled Pearson's χ^2	AIC
Change in surface area Change in surface area^2	1.09	872.7
Physiographic region • Wetland class	1.08	881.8
Global model	1.08	885.8

Note: Pearson's chi-square statistics are from a generalized linear mixed model specified for a negative binomial distribution.

TABLE 2
FACTORS AFFECTING NUMBER OF YEARS USED BY LESSER SCAUP IN EASTERN SOUTH DAKOTA, 1987–2002

Variables	df	β	P
Intercept	204	1.0634	<0.0001
Change in surface area	204	0.017	<0.0001
Change in surface area^2	204	-0.00004	<0.0001

Note: Parameter estimates and test statistics are from a generalized linear mixed model specified for a negative binomial distribution.

TABLE 3
AKAIKE'S INFORMATION CRITERION MODEL WEIGHTS OF FACTORS AFFECTING LONG-TERM WETLAND USE BY LESSER SCAUP IN EASTERN SOUTH DAKOTA, 1987–2002

Variable	AIC ω_i
Change in surface area	0.99
Physiographic region	0.01
Average wetland area	0.001

breeding success, and survival (e.g., Ebbinge and Spaans 1995; Mainguy et al. 2002). Brasher (2010) reported that duck use decreased as wetlands became more isolated. Greater isolation may increase distances between stopover wetlands, increasing flight paths and placing additional energetic burdens on birds en route to breeding grounds. However, effects of longer flight paths on birds' ability to sequester sufficient food and maintain body condition remain uninvestigated. Nonetheless, it is likely that waterfowl populations have adapted to the variable dry-wet climate of the Prairie Pothole Region, and population numbers have been observed to respond accordingly.

The relationship between breeding ducks and wetland availability in the Prairie Pothole Region (indexed as "May Ponds") is well documented (Batt et al. 1989), but it is rarely applied to spring migrant use. During wet periods, wetlands in the Prairie Pothole Region expand in surface area and even overflow their basins (Leibowitz and Vining 2003; Tiner 2003; Shapley et al. 2005). Precipitation generally increased across the Prairie Pothole Region during the 20th century, with the highest recorded rainfall in the southeastern region. Analysis of climate trends indicate that average annual rainfall in eastern South Dakota varied within a range of 500–600 mm/yr with the highest precipitation occurring in the mid- to late 1990s (Garbrecht and Rossel 2002; Millet et al. 2009). We demonstrated that lesser scaup numbers in eastern South Dakota were positively related to wetland size and that wetland size was positively related to precipitation.

The relationship between lesser scaup numbers and wetland variability was quadratic, indicating a preference for wetlands that exhibited intermediate levels of surface area fluctuation. We found that permanent wetlands exhibited higher surface area variability than semipermanent, seasonal, and temporary wetlands, which may be linked to the fact that they are generally larger than other wetland classes. The relatively large size may also ensure longer hydroperiods and thus provide refugia during droughts. Longer hydroperiods are critical to the survival of specific aquatic invertebrates (e.g., amphipods) that constitute a large proportion of scaup diets during migration (Anteau and Afton 2004; Strand et al. 2007). We suggest that studies conducted in regions where semipermanent wetlands are more common, and during average or above-average water condition years, may overestimate their importance to lesser scaup.

Over the 16-year survey period, permanent wetlands in the Prairie Coteau experienced the greatest variation in size from dry to wet periods. High wetland density and

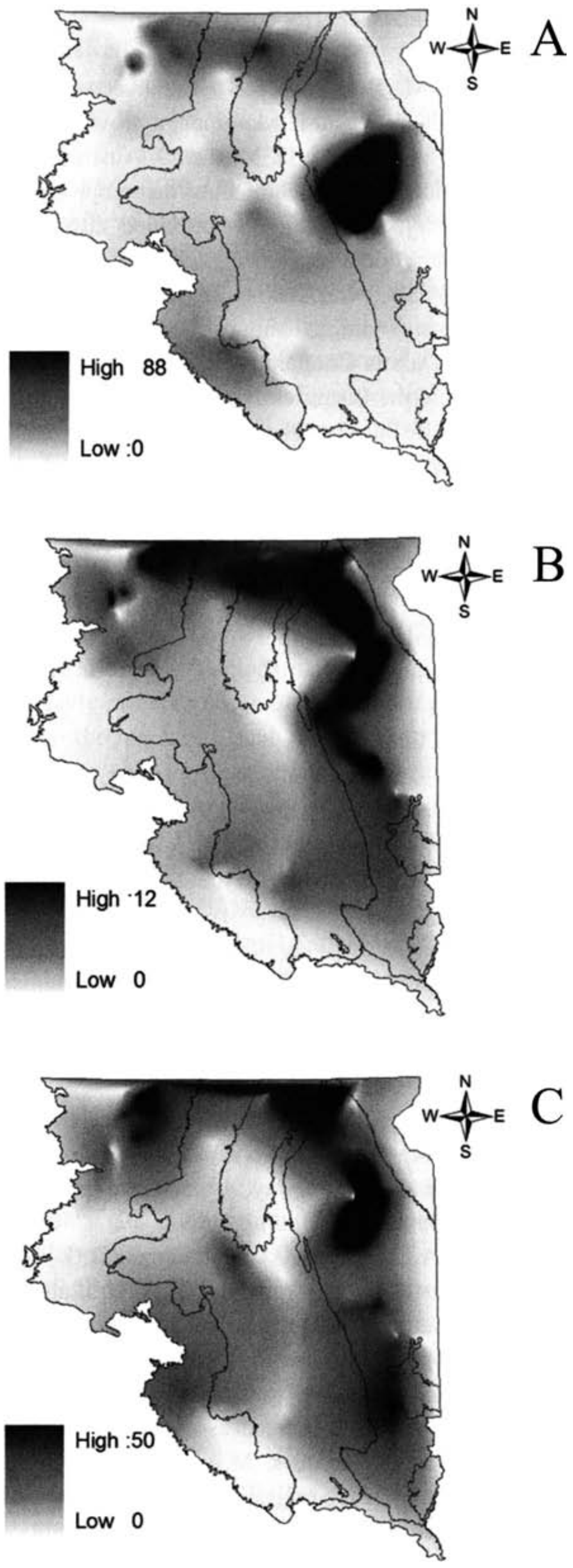

Figure 5. Spatial distribution showing (A) average change in surface area (ha) at each four-square-mile plot surveyed from 1987 to 2002 in eastern South Dakota, (B) average number of years used by migrant lesser scaup, and (C) average number of lesser scaup counted.

TABLE 4
ODDS RATIO ESTIMATES OF LONG-TERM USE OF PHYSIOGRAPHIC REGIONS BY LESSER SCAUP IN EASTERN SOUTH DAKOTA, 1987–2002

Effect	Point estimate	95% confidence limits	
Missouri Coteau vs. Prairie Coteau	0.966	0.697	1.337
Minnesota Red River Lowland vs. Prairie Coteau	0.503	0.206	1.229
Lake Dakota Plain vs. Prairie Coteau	0.431	0.137	1.358
James River Lowland vs. Prairie Coteau	0.488	0.292	0.816

Note: Estimates are based on a logistic model of the proportion of years used.

TABLE 5
ODDS RATIO ESTIMATES OF LONG-TERM USE OF WETLAND CLASSES BY LESSER SCAUP IN EASTERN SOUTH DAKOTA, 1987–2002

Effect	Point estimate	95% confidence limits	
Temporary vs. permanent	0.057	0.033	0.097
Seasonal vs. permanent	0.143	0.113	0.181
Semipermanent vs. permanent	0.28	0.233	0.336

Note: Estimates are based on a logistic model of used vs. unused wetlands.

hydrodynamics have been linked to increased productivity (van der Valk 1989; Johnson et al. 2004). Dynamic surface water levels increase sediment exposure and reinundation, thereby facilitating nutrient cycling and productivity (Mitsch and Gosselink 2007). The period of flooding after sediment exposure is usually followed by rapid and prolific plant growth fueled by the increased nutrient availability (van der Valk and Davis 1978), which contributes to increased secondary and tertiary productivity farther up the food chain (Euliss et al. 2004). Our study also determined that contrary to previous research (e.g., Lindeman and Clark 1999; Mockler 2004), permanent wetlands were more likely to be used by migrant scaup than semipermanent wetlands over the long term.

Observed differences in wetland use may be an artifact of sampling location and timing, as wetland hydroperiods tend to shift depending on local climate. Also, wetland resources and types are not evenly distributed across the Prairie Pothole Region (Kahara et al. 2009). Few lesser scaup breed in South Dakota; however, it is major stopover site for spring migrants (Holland 1997). Our study suggests that dynamic permanent wetlands may provide more benefits to migrating lesser scaup over the long term.

We suggest that the northern portions of the Prairie Coteau be considered an area of conservation concern for migrating lesser scaup. This region is not only rich in large, aerially dynamic permanent wetlands but also has large numbers of semipermanent wetlands favored by lesser scaup in average and above-average water condition years. This area is also an important staging and brood-rearing area for other diving duck species including ring-necked ducks (*Aythya collaris*), redheads (*Aythya americana*), and buffleheads (*Bucephala albeola*) (Holland 1997). Conservation programs such as the Conservation Reserve Program (CRP) and the Wetlands Reserve Program (WRP) have enrolled millions of hectares of land since their inception in the early 1990s. These programs have reportedly significantly boosted waterfowl productivity (Reynolds et al. 2001) resulting in millions of new ducks each year. Although wetland losses in the Dakotas have been relatively small compared to other regions of the Prairie Pothole Region (35% in South Dakota and 49% in North Dakota), these regions also likely provide the most productive waterfowl habitats in the region (Johnson et al. 2005). Therefore, the weight of these wetland losses may be more ecologically severe.

Hydrodynamics are not currently considered as part of the criteria for conservation prioritization in the Prairie Pothole Region and warrant further investigation. Our data support studies that link dynamic climate conditions to habitat suitability for waterfowl (e.g., Johnson et al. 2005). Under current global climate change scenarios, hydrologically dynamic wetland areas could shift farther east in the Prairie Pothole Region to areas that have already lost the majority of their wetlands (Dahl 1990). In addition to focusing on breeding sites, the inclusion of wetlands located along spring migration routes should be considered as part of conservation planning to improve lesser scaup survival and breeding success. The criteria we identified may be used to identify important lesser scaup habitats in other regions in the Prairie Pothole Region.

ACKNOWLEDGMENTS

We thank M. Bouchard for assistance with maps and GIS data. S. Vaa and P. Mammenga provide technical assistance in the field. D. Mushet, J. Austin, and R. Murano provided helpful comments that improved the manuscript. Project funding was provided through the Wildlife Restoration Program (W-75-R-150-75110) administered by the South Dakota Department of Game, Fish, and Parks. Additional support was provided by the USGS South Dakota Cooperative Fish and Wildlife Research Unit and the Bismarck HAPET Office of the U.S. Fish and Wildlife Service. The South Dakota Cooperative Fish and Wildlife Research Unit is jointly supported by the U.S. Geological Survey, South Dakota State University, South Dakota Department of Game, Fish, and Parks, the Wildlife Management Institute, and the U.S. Fish and Wildlife Service. Any use of trade names is for descriptive purposes only and does not imply endorsement by the federal government.

REFERENCES

Allen, A.W. 1986. *Habitat suitability index models: lesser scaup (breeding)*. U.S. Fish and Wildlife Service. Biological Report. Department of the Interior, Washington, DC.

Anteau, M.J. 2006. Ecology of lesser scaup and amphipods in the upper Midwest: Scope and mechanisms of the spring condition hypothesis and implications for migration habitat conservation. PhD diss., Louisiana State University, Baton Rouge.

Anteau, M.J., and A.D. Afton. 2004. Nutrient reserves of lesser scaup *Aythya affinis* during spring migration in the Mississippi Flyway: A test of the spring condition hypothesis. *The Auk* 121:917–29.

Austin, J.E., A.D. Afton, M.G. Anderson, R.G. Clark, C.M. Custer, J.S. Lawrence, J.B. Pollard, and J.K. Ringleman. 1999. Declines of Greater and Lesser scaup populations: Issues, hypotheses, and research directions. http://www.npwrc.usgs.gov/resource/birds/blubill/index.htm (accessed January 1, 2009).

Austin, J.E., D.A. Granfors, M.A. Johnson, and S.C. Kohn. 2002. Scaup migration patterns in North Dakota relative to temperatures and water conditions. *Journal of Wildlife Management* 66:874–82.

Baar, L., R.S. Matlack, W.P. Johnson, and R.B. Barron. 2008. Migration chronology of waterfowl in the southern High Plains of Texas. *Waterbirds* 31:394–401.

Batt, B.D.J., M.G. Anderson, C.D. Anderson, and F.D. Caswell. 1989. The use of prairie potholes by North American ducks. In *Northern Prairie Wetlands*, ed. A. Van der Valk, 204–27. Iowa State University Press, Ames.

Brasher, M.G. 2010. Duck use and energetic carrying capacity of actively and passively managed wetlands in Ohio during autumn and spring migration. PhD diss., Ohio State University, Columbus.

Burnham, K.P., and D.R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical-Theoretic Approach*, 2nd ed. Springer-Verlag, New York.

Dahl, Thomas E. 1990. Wetlands losses in the United States 1780s to 1980s. http://www.npwrc.usgs.gov/resource/wetlands/wetloss/index.htm (accessed August 1, 2010).

Diaz, H.F. 1986. An analysis of twentieth century climate fluctuations in northern North America. *Journal of Climate and Applied Meteorology* 25:1625–57.

Ebbinge, B.S., and B. Spaans. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied brent geese *Branta b. bernicla* in the high Arctic. *Journal of Avian Biology* 26:105–13.

Euliss, N.H., Jr., J.W. LaBaugh, L.H. Fredrickson, D.M. Mushet, G.A. Swanson, T.C. Winter, D.O. Rosenberry, and R.D. Nelson. 2004. The wetland continuum: A conceptual framework for interpreting biological studies in the prairie pothole region of North America. *Wetlands* 24:448–58.

Euliss, N.H., Jr., D.M. Mushet, and D.A. Wrubleski. 1999. Wetlands of the prairie pothole region: Invertebrate species composition, ecology, and management. In *Invertebrates in Freshwater Wetlands of North America: Ecology and Management*, ed. D.P. Batzer, R.B. Rader, and S.A. Wissinger, 471–514. John Wiley and Sons, New York.

Flint, R.F. 1971. *Glacial and Quaternary Geology*. John Wiley and Sons, New York.

Garbrecht, J.D., and F.E. Rossel. 2002. Decade-scale precipitation increase in Great Plains at the end of the 20th century. *Journal of Hydrological Engineering* 7:64–75.

Gleason, R.A., and N. Euliss. 1998. Sedimentation of prairie wetlands. *Great Plains Research* 8:97–112.

Haukos, D.A., M.R. Miller, D.L. Orthmeyer, J.Y. Takekawa, J.P. Fleskes, M.L. Casazza, W.M. Perry, and J.A. Moon. 2006. Spring migration of northern pintails from Texas and New Mexico, USA. *Waterbirds* 29:127–36.

Holland, M.M. 1997. Characteristics of wetlands used by breeding diving ducks in eastern South Dakota. Master's thesis, South Dakota State University, Brookings.

Hupp, J.W., N. Yamaguchi, P.L. Flint, J.M. Pearce, K. Tokita, T. Shimada, A.M. Ramey, S. Kharitonov, and H. Higuchi. 2011. Variation in spring migration routes and breeding distribution of northern pintails *Anas acuta* that winter in Japan. *Journal of Avian Biology*, http://onlinelibrary.wiley.com/doi/10.1111/j.1600-048X.2011.05320.x/full (accessed August 1, 2010).

Johnson, R.R., and K.F. Higgins. 1997. Wetland resources of eastern South Dakota. PhD diss., South Dakota State University, Brookings.

Johnson, W.C., B. Werner, G.R. Guntenspergen, R.A. Voldseth, B. Millett, D.E. Naugle, M. Tulbure, R.W.H. Carroll, J. Tracy, and C. Olawsky. 2010. Prairie wetland complexes as landscape functional units in a changing climate. *BioScience* 60:128–40.

Johnson, W.E., S.E. Boettcher, K.A. Poiani, and G.R. Guntenspergen. 2004. Influence of weather extremes on the hydrology of glaciated prairie wetlands. *Wetlands* 24:385–98.

Johnson, W.E., B.V. Millett, T. Gilmanov, R.A. Voldseth, G.R. Guntenspergen, and D.E. Naugle. 2005. Vulnerability of northern prairie wetlands to climate change. *BioScience* 55:863–72.

Kahara, S.N., R.M. Mockler, K.F. Higgins, S.R. Chipps, and R.R. Johnson. 2009. Spatiotemporal patterns of wetland occurrence in the Prairie Pothole Region of eastern South Dakota. *Wetlands* 29:678–89.

Kantrud, H.A., and R.E. Stewart. 1977. Use of natural basin wetlands by breeding waterfowl in North Dakota. *Journal of Wildlife Management* 41:243–53.

Krapu, G., P. Pietz, D. Brandt, and R. Cox, Jr. 2006. *Mallard Brood Movements, Wetland Use, and Duckling Survival During and Following a Prairie Drought.* Northern Prairie Wildlife Research Center, USGS, Jamestown, ND.

LaBaugh, J.W., T.C. Winter, G.A. Swanson, D.O. Rosenberry, R.D. Nelson, and N.H. Euliss, Jr. 1996. Changes in atmospheric circulation patterns affect mid-continent wetlands sensitive to climate. *Limnology and Oceanography* 41:864–70.

Leibowitz, S.G., and K.C. Vining. 2003. Temporal connectivity in a prairie pothole complex. *Wetlands* 23(1):13–25.

Lindeman, D.H., and R.G. Clark. 1999. Amphipods, land–use impacts, and lesser scaup *Aythya affinis*

distribution in Saskatchewan wetlands. *Wetlands* 19:627–38.

Mainguy, J., J. Bêty, G. Gauthier, and J.-F. Giroux. 2002. Are body condition and reproductive effort of laying greater snow geese affected by the spring hunt? *Condor* 104:156–61.

Millett, B., W.C. Johnson, and G. Guntenspergen. 2009. Climate trends of the North American prairie pothole region, 1906–2000. *Climatic Change* 93:243–67.

Mitsch, W.J., and J.G. Gosselink. 2007. *Wetlands,* 4th ed. John Wiley and Sons, New York.

Mockler, R.E. 2004. Lesser scaup use of wetlands in eastern South Dakota. Master's thesis, South Dakota State University, Brookings.

Naugle, D.E., R.R. Johnson, T.R. Cooper, M.M. Holland, and K.F. Higgins. 2000. Temporal distribution of waterfowl in eastern South Dakota: Implications for aerial surveys. *Wetlands* 20:177–183.

Neely, R.K., and J.L. Baker. 1989. Nitrogen and phosphorus dynamics and the fate of agricultural runoff. In *Northern Prairie Wetlands*, ed. A. van der Valk, 92–131. Iowa State University Press, Ames.

Pedan, A. 2001. Analysis of count data using the SAS system. In *Proceedings of the Twenty-Sixth Annual SAS Users Group International Conference*. SAS Institute, Cary, NC.

Prairie Pothole Joint Venture. 2003. Prairie Pothole Joint Venture. http://www.ppjv.org/pdf/15year.pdf (accessed August 1, 2010).

Raveling, D.G., and M.E. Heitmeyer. 1989. Relationships of population size and recruitment of pintails to habitat conditions and harvest. *Journal of Wildlife Management* 53:1088–1103.

Reynolds, R.E., T.L. Shaffer, R.W. Renner, W.E. Newton, and B.D.J. Batt. 2001. Impact of the Conservation Reserve Program on duck recruitment in the U.S. Prairie Pothole Region. *Journal of Wildlife Management* 65:765–80.

SAS Institute. 2004. The SAS system for windows. SAS Institute, Cary, NC.

Shapley, M.D., W.C. Johnson, D.R. Engstrom, and W.R. Osterkamp. 2005. Late-Holocene flooding and drought in the Northern Great Plains, USA, reconstructed from tree rings, lake sediments, and ancient shorelines. *Holocene* 15:29–41.

Smith, A.G. 1971. *Ecological Factors Affecting Waterfowl Production in the Alberta Parklands*. Resource Publication Number 98. U.S. Fish Wildlife Service, Washington, DC.

Stewart, R.E., and H.A. Kantrud. 1971. *Classification of Natural Ponds and Lakes in the Glaciated Prairie Region*. Resource Publication Number 92. U.S. Fish and Wildlife Service, Washington, DC.

Strand, K.A., S.R. Chipps, S.N. Kahara, K.F. Higgins, and S. Vaa. 2007. Patterns of prey use by lesser scaup *Aythya affinis* (Aves) and diet overlap with fishes during spring migration. *Hydrobiologia* 598:389–98.

Tiner, R.W. 2003. Geographically isolated wetlands of the United States. *Wetlands* 23:494–516.

USFWS (U.S. Fish and Wildlife Service). 2010. *Waterfowl Population Status, 2010*. U.S. Department of the Interior, Washington, DC.

van der Valk, A.G. 1989. *Northern Prairie Wetlands*. Iowa State University Press, Ames.

van der Valk, A.G., and C.B. Davis. 1978. The role of the seed bank in the vegetation dynamics of prairie glacial marshes. *Ecology* 59:322–35.

Winter, T.C. 1989. Hydrologic studies of wetlands in the Northern Prairie. In *Northern Prairie Wetlands*, ed. A. van der Valk, 16–54. Iowa State University Press, Ames.

Winter, T.C., and D.O. Rosenberry. 1998. Hydrology of prairie pothole wetlands during drought and deluge: A 17-year study of the cottonwood lake wetland complex in North Dakota in the perspective of longer term measured and proxy hydrological records. *Climatic Change* 40:189–209.