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Management and Conservation Article

Effects of Local and Landscape Variables on Wetland Bird Habitat Use During Migration Through the Rainwater Basin

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ABSTRACT Staging areas and migratory stopovers of wetland birds can function as geographic bottlenecks; common dependence among migratory wetland bird species on these sites has major implications for wetland conservation. Although 90% of playa wetlands in the Rainwater Basin (RWB) region of Nebraska, USA, have been destroyed, the area still provides essential stopover habitat for up to 10 million waterfowl each spring. Our objectives were to determine local (within wetland and immediate watershed) and landscape-scale factors influencing wetland bird abundance and species richness during spring migration at RWB playas. We surveyed 36–40 playas twice weekly in the RWB and observed approximately 1.6 million individual migratory wetland birds representing 72 species during spring migrations 2002–2004. We tested a priori hypotheses about whether local and landscape variables influenced overall species richness and abundance of geese, dabbling ducks, diving ducks, and shorebirds. Wetland area had a positive influence on goose abundance in all years, whereas percent emergent vegetation and hunting pressure had negative influences. Models predicting dabbling duck abundance differed among years; however, individual wetland area and area of semipermanent wetlands within 10 km of the study wetland consistently had a positive influence on dabbling duck abundance. Percent emergent vegetation also was a positive predictor of dabbling duck abundance in all years, indicating that wetlands with intermediate (50%) vegetation coverage have the greatest dabbling duck abundance. Shorebird abundance was positively influenced by wetland area and number of wetlands within 10 km and negatively influenced by water depth. Wetland area, water depth, and area of wetlands within 10 km were all equally important in models predicting overall species richness. Total species richness was positively influenced by wetland area and negatively influenced by water depth and area of semipermanent wetlands within 10 km. Avian species richness also was greatest in wetlands with intermediate vegetation coverage. Restoring playa hydrology should promote intermediate percent cover of emergent vegetation, which will increase use by dabbling ducks and shorebirds, and decrease snow goose (*Chen caerulescens*) use of these wetlands. We observed a reduction in dabbling duck abundance on wetlands open to spring snow goose hunting and recommend further investigation of the effects of this conservation order on nontarget species. Our results indicate that wildlife managers at migration stopover areas should conserve wetlands in complexes to meet the continuing and future habitat requirements of migratory birds, especially dabbling ducks, during spring migration.

KEY WORDS habitat use, migration, Nebraska, playas, Rainwater Basin, wetland birds.

Although spring migration is an essential activity for most wetland bird species, ecology of migrating birds in their stopover habitat is poorly understood (Arzel et al. 2006, Drent et al. 2006, Newton 2006). At least 25 waterfowl species and 38 shorebird species use wetlands in the Great Plains as stopover sites during spring migration (Skagen 1997, Smith 2003, Jorgensen 2004). Many of these wetland birds are long-distance migrants that rely on wetland stopover sites along the migration route to accumulate critical energy reserves (Myers et al. 1987, LaGrange and Dinsmore 1988, Krapu et al. 1995, Davis and Smith 1998*a*). These wetlands are considered crucial feeding and resting areas that function as part of the stepping stone system of wetlands necessary for wetland birds to complete migration (Myers et al. 1987, LaGrange and Dinsmore 1988, Skagen and Knopf 1993).

Despite a 90% decrease in the number of wetlands and 88% decrease in wetland area, the Rainwater Basin (RWB) region of south-central Nebraska, USA, provides an essential link between wintering and breeding areas for 7–10 million waterfowl every spring, including virtually all of the 600,000 midcontinental greater white-fronted geese (*Anser albifrons*), 500,000 Canada geese (*Branta canadensis*), 50% of midcontinent mallards (*Anas platyrhynchos*), and 30% of continental northern pintails (*A. acuta*; Gersib et al. 1992). Although less is known about use of RWB playas by nonwaterfowl species, the wetlands provide habitat for 38 shorebird species (Jorgensen 2004) and the endangered whooping crane (*Grus americana*; Austin and Richert 2001).

Staging areas and migratory stopovers often function as geographic bottlenecks. Entire populations within a flyway can be affected by the quality and quantity of available wetland habitat at stopover sites (Myers 1983). This common dependence among migratory birds on staging sites has major implications for wetland conservation and restoration (e.g., Skagen 1997); however, factors that influence habitat use for this variety of taxa during migration are relatively unknown. Most evaluations of wetland bird habitat use and community composition from a landscape perspective focus on breeding birds (Brown and Dinsmore 1986, Naugle et al. 2000, Fairbairn and Dinsmore 2001, Naugle et al. 2001). Moreover, little is known about the effects of local and landscape-scale habitat characteristics on wetland bird distribution during migration. Our goal was to identify habitat characteristics of wetlands used by wetland birds during migration. Specifically we examined local

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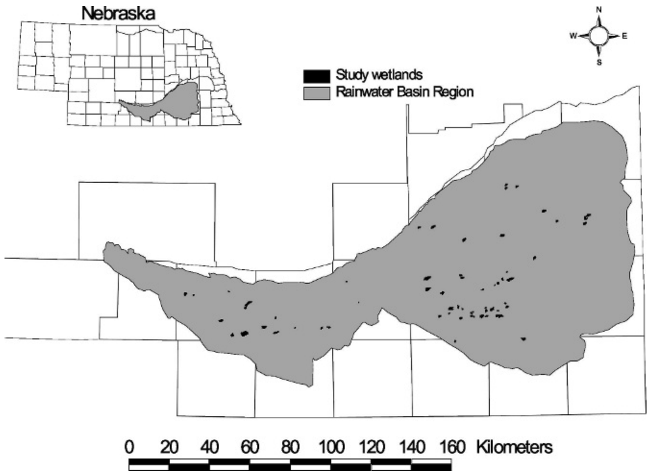

Figure 1. Rainwater Basin sample wetlands located in south-central Nebraska, USA, where influences of local and landscape level wetland variables on migratory wetland bird habitat use, abundance, and species richness were evaluated during springs 2002–2004.

(within wetland and immediate watershed) and landscape factors influencing abundance and species richness of wetland birds during spring migration within the RWB.

STUDY AREA

Wetlands in the RWB were classified as playas and distributed among 21 counties in south-central Nebraska (LaGrange 2005; Fig. 1). The RWB region was characterized by flat to gently rolling loess plains, with elevations ranging from 455 m in the east to 758 m in the west (Gersib et al. 1989). Most RWB wetlands ranged from <1 ha to 16 ha, although several wetlands were >400 ha (Brennan et al. 2005). Located primarily on silt loam and silty clay loam soils, RWB playas were shallow depressions likely formed by wind scouring (Kuzila 1994).

Soil surveys from 1910 to 1917 indicated the RWB contained 11,000 wetlands over approximately 82,000 ha; however, conversion to agricultural land has destroyed >90% of wetlands and 88% of original wetland area (Raines et al. 1990, Bishop and Vrtiska 2008). Among the remaining RWB wetlands, 80% have undergone reductions in size, loss of available water, and mechanical modifications to facilitate drainage (Schildman and Hurt 1984, Smith and Higgins 1990). In addition to elimination or alteration of most playas in the RWB, the associated watersheds have also been modified. Conversion of the surrounding landscape from prairie to crop fields has altered timing and magnitude of water runoff, as have water additions by conservation agencies, which in turn influences individual wetland hydrological conditions.

Annual precipitation in Clay County, which contained the most surveyed wetlands, was 53.4 cm in 2002, 49.7 cm in 2003, and 59.7 cm in 2004 (National Oceanic and Atmospheric Administration 2005). All years of study received below average precipitation relative to the 30-year mean (70 cm; National Oceanic and Atmospheric Administration 2005; Clay County, NE). Based on aerial surveys of public wetlands conducted in mid-March, wetland availability also differed among study years, with 1,500 ha, 1,200 ha, and 2,550 ha of flooded wetland habitat available in 2002, 2003, and 2004, respectively (J. Drahota, United States Fish and Wildlife Service [USFWS], Kearney, NE, personal communication). Public wetlands made up 86%, 95%, and 80% of our sampled wetlands in 2002, 2003, and 2004, respectively.

METHODS

Data Collection

Wetland selection.—We surveyed wetlands for the presence of migratory wetland birds during 3 spring (mid-Feb–mid-May) migrations 2002–2004. We randomly selected wetlands at the beginning of each field season from the pool of available wetlands containing water within the study area. We located potential study wetlands using maps of hydric soils, and we visually assessed the wetlands for ice and hydric vegetation in early February 2002–2004. We sampled 36 wetlands in 2002 and 2003 and 40 wetlands in 2004.

Migratory bird surveys.—Two observers working separately surveyed wetlands twice weekly to quantify wetland bird use; however, we only surveyed <10% of wetlands once in some weeks due to logistical constraints and evaporation. We divided daylight hours into 4 time intervals: sunrise to 0800 hours, 0800–1200 hours, 1200–1600, and 1600 hours to sunset, and we sampled wetlands randomly during 2 different time intervals each week.

We used several survey methods to detect waterfowl and shorebirds within wetlands. We surveyed waterfowl with a modified spring count protocol of the USFWS and Canadian Wildlife Service (1987). Before entering a wetland, we recorded all birds visible in open water, which we observed from a vantage point. To detect smaller or more secretive species (i.e., some shorebirds [Charadriiformes], bitterns and wading birds [Ardeidae]), we then visited a set of pre-established points within the wetland. We spent 10 minutes at each point, recorded additional visible species, and estimated the number of each species. In some cases, we observed birds from the initial vantage point, and visiting survey points did not alter initial counts. However, in more densely vegetated or larger wetlands, we sometimes failed to observe some birds from the vantage point and could only detect birds from survey points within the wetland. To ensure consistent sampling effort, we varied the number of points we visited per wetland according to the size of the wetland: 1 point in wetlands $\leq$5 ha; 2 points in wetlands 5.1–25 ha; 3 points in wetlands 25.1–100 ha; and 4 points in wetlands >100 ha (Brown and Dinsmore 1986, O'Neal et al. 2008). Areal coverage ranged from nearly 100% at small sites to <2% at larger wetlands. We compensated for less areal coverage by increased detection of birds as we moved among survey points; larger sites had more survey points, which increased effective coverage (Brown and Dinsmore 1986).

In flocks with <100 birds, we recorded wetland bird species and the individual number of each species. In flocks with >100 birds, we recorded wetland bird species and visually estimated the number of individual species. We included birds we observed while walking between observation points within a wetland in the overall count for the wetland (Fairbairn and Dinsmore 2001). However, if previously counted birds flew to another part of the wetland, we did not include them.

Local wetland characteristics.—We measured 15 local variables at each wetland to quantify wetland habitat characteristics. During each survey, we estimated the percent of the wetland basin containing water (% full) by comparing current water conditions with digital aerial photographs and the extent of the wetland plant boundary. Following completion of avian surveys in mid-May, we measured percent of wetland area (based on wetted area) containing emergent vegetation in 1 of 7 categories: <1%, 1–5%, 6–25%, 26–50%, 51–75%, 76–95%, and >95% (Fairbairn and Dinsmore 2001). Dabbling duck density often is greatest in wetlands with intermediate emergent vegetation coverage (50%) and least in wetlands with sparse or dense vegetation coverage (Weller and Fredrickson 1974); therefore, we also included a variable that was the arcsine transformation of the percentage of vegetation to reflect the polynomial relationship between dabbling duck abundance and vegetation. We used 2 measures of wetland vegetation: the polynomial measure to predict taxa we expected to use wetlands with intermediate vegetation coverage (i.e., dabbling ducks, shorebirds), and the linear measure to predict taxa we expected to use wetlands with either dense or sparse vegetation coverage (i.e., geese).

We established a north–south transect within each wetland to survey wetland vegetation in mid-May. If the transect was $\leq$800 m, we established data collection points every 50 m; however, for wetlands with transects >800 m, we established data collection points every 100 m, with minimum transect length $\geq$200 m. At each designated collection point on a transect we recorded all plant species that covered >10% of the groundcover in a 1 $\times$ 1 m plot, and we classified the plant community at that location as 1 of 5 vegetation zones: upland, transition, outer marsh, persistent emergent, or inner marsh (Gilbert 1989).

We used the plant data to calculate the percentage of wetland vegetation that composed each of the 5 vegetation zones within the wetland. The upland zone included native and planted prairie stands; the transition zone consisted of mesic and wet-mesic stands of grasses, sedges, and forbs; the outer marsh zone contained spikerush (*Eleocharis* spp.), hydric grasses, and forbs; the persistent emergent zone consisted of sedges (*Cyperaceae*) and cattail (*Typhaceae*); and the inner marsh zone included drawdown (e.g., *Saggitaria* spp.) and aquatic bed species (e.g., *Azolla mexicana* and *Lemna* spp.; Gilbert 1989). We determined the percentage of each vegetation zone within the wetland by dividing the number of transect locations classified as a given vegetation zone by the total number of transect locations. We also measured water depth along the vegetation transect at each wetland. We recorded water depth at 5 random locations on transects where we encountered water. We measured water depth to the nearest centimeter and averaged it for each wetland.

Landscape-scale variables.—We measured 11 landscape variables associated with each wetland at 2 spatial scales: 5-km and 10-km buffers around the wetland perimeter. We selected these scales based on the cruising range (i.e., the distance birds fly between wetlands within a stopover site), which is commonly used to define proper scale for landscape analysis (Wiens et al. 1986). Specifically, we selected these distances because most (80%) northern pintail evening flights in the RWB were <5 km (Cox and Davis 2002), while most (90%) shorebirds traveled <10 km between wetlands at stopover sites (Farmer and Parent 1997). We analyzed a land cover dataset (1991–1993) provided by the GAP project of Nebraska (Henebry et al. 2005) and a hydric soils dataset provided by the Natural Resources Conservation Service to describe landscape characteristics. The land cover dataset classified the RWB landscape into 7 habitat categories: cropland, developed land, open water, range and grassland, riparian, trees and shrubs, and wetlands; however, we analyzed only cropland, grassland, riparian, and wetland habitats. We only analyzed semipermanent wetlands (Cowardin et al. 1979) from the hydric soils dataset to account for drought conditions and limited wetland availability. We used PatchAnalyst (ArcView version 3.2; Environmental Systems Resource Institute, Redlands, CA) to calculate area for each land use category in the land cover data. We also used PatchAnalyst to calculate area and number of wetlands for the hydric soil data layer within 5 km and 10 km of each sample wetland perimeter.

Analytical Approach

We grouped avian abundance data into 4 taxonomic groups based on foraging strategies (Bellrose 1980) and migration chronology (Brennan 2006): geese, dabbling ducks, diving ducks, and shorebirds. We calculated abundance annually by summing the number of birds within each group that we observed at a wetland. Due to differences in precipitation among years, which resulted in differences in wetland availability, we analyzed data separately from each year. We modeled avian abundance instead of density because we hypothesized that wetland area would be an important factor influencing abundance and may be of conservation concern (Brown and Dinsmore 1986, McKinney et al. 2006). We determined species richness for each wetland based on the total number of species we observed during each migration period.

We used an information-theoretic approach to evaluate factors associated with abundance and species richness of migratory birds. Specifically, we used combinations of the following local and landscape wetland characteristics to construct a priori candidate models explaining abundance by taxonomic group (birds/wetland/yr), as well as species richness (Table 1): 1) Wetland area (AREA). We hypothesized abundance and species richness would increase with wetland area because generally, species richness increases with habitat area (MacArthur and Wilson 1967, Rosenzweig 1995). 2) Emergent vegetation [EMERVER(LIN) and EMERVEG(SIN)]. We hypothesized cover of emergent vegetation would be an important local factor

Table 1. Predictive models developed to identify local- and landscape-level habitat characteristics important for different taxa of wetland birds during migration through the Rainwater Basin region of Nebraska, USA, February–May 2002–2004.

Dependent variable	Factors hypothesized to explain variation in dependent variable
Goose[a] abundance	Wetland area, open to hunting, water depth, area of cropland within 5 km, and % emergent vegetation.
Dabbling duck[b] abundance	Wetland area, area of semipermanent wetlands within 10 km, area of cropland within 10 km, open to hunting, and % emergent vegetation.
Diving duck[c] abundance	Wetland area, water depth, % vegetation classified as inner marsh, and area of riparian habitat within 5 km.
Shorebird[d] abundance	Wetland area, water depth, % emergent vegetation, and no. of wetlands within 10 km.
Species richness	Wetland area, water depth, area of grassland within 5 km, area of semipermanent wetlands within 10 km, area of semipermanent wetlands within 5 km.

[a] Greater white-fronted goose, snow and Ross' geese (*Chen* spp.), and Canada goose (*Branta canadensis*).

[b] Wood duck (*Aix sponsa*), gadwall (*Anas strepera*), American wigeon (*A. americana*), mallard (*A. platyrhynchos*), blue-winged teal (*A. discors*), northern shoveler (*A. clypeata*), northern pintail, American green-winged teal (*A. crecca*).

[c] Canvasback (*Aythya valisineria*), redhead (*A. americana*), ring-necked duck (*A. collaris*), lesser scaup (*A. affinis*), bufflehead (*Bucephala albeola*), common goldeneye (*Bucephala clangula*), hooded merganser (*Lophodytes cucullatus*), common merganser (*Mergus merganser*), red-breasted merganser (*M. serrator*), ruddy duck (*Oxyura jamaicensis*).

[d] Charadriinae, Recurvirostridae, Scolopacidae, and Phalaropodinae families.

influencing bird use on migration areas, similar to breeding and wintering areas (VanRees-Siewert and Dinsmore 1996, Fairbairn and Dinsmore 2001, Conway et al. 2005). 3) Hunting pressure (HUNT). We hypothesized hunting pressure (whether a wetland was open or closed to spring snow goose hunting) would affect goose and dabbling duck distribution because regional hunting can reduce the number of wetland birds using an area (Percival et al. 1997). Waterfowl increase use of refuges and protected areas when disturbed; snow geese (*Chen caerulescens*; Bélanger and Bedard 1989) and Ross's geese (*C. rossi*; Taylor and Kirby 1990) both responded to hunting disturbance by using protected areas. Although spring migration does not often coincide with typical waterfowl hunting seasons, the spring light goose conservation order (spring hunting seasons for snow geese) has been implemented in Nebraska and other regions by the USFWS in an attempt reduce populations of lesser snow geese. 4) Water depth (WATER1 [mean water depth] and WATER2 [max. water depth]). We hypothesized goose and shorebird abundance would decrease with water depth because water depth influences wetland bird abundance and habitat use on wintering areas (Colwell and Taft 2000, Isola et al. 2000). 5) Wetland area in the surrounding landscape (SEMI-PERM). We hypothesized that dabbling duck abundance and species richness would increase with amount of wetland area within 10 km because of the amount of nearby wetland habitat influences wetland bird species richness and occurrence on nesting areas (Brown and Dinsmore 1986). 6) Cropland in the surrounding landscape (CROP). We hypothesized that the amount of cropland in the surrounding landscape would influence goose and dabbling duck abundance because geese use grain fields primarily for foraging during migration (Frederick and Klaas 1982, Alisauskas and Ankney 1992) and agricultural grains, specifically corn, are an important component in the diets of dabbling ducks during migration (Jorde et al. 1983, LaGrange 1985). 7) Percent inner marsh (%IM). Plants found in the inner marsh vegetation zone included several species that comprise a majority of several diving duck diets, including arrowhead (*Saggitaria* spp.) and chufa flatsedge (*Cyperus esculentus*; Moore et al. 1998). Several diving duck species also prefer winter habitats that included submergent vegetation and open water, compared to more shallow habitats containing emergent vegetation (Bergan and Smith 1989). Therefore, we hypothesized diving duck abundance would increase with percent inner marsh vegetation. 8) Grassland in the surrounding landscape within 5 km (GRASS). We hypothesized species richness would increase with amount of grassland in the surrounding landscape because area of grassland habitat surrounding wetlands has been correlated with occurrence of 9 breeding bird species (Naugle et al. 2000).

Statistical Analyses

We used multiple linear regression to test a priori models for all dependent variables and then selected the most parsimonious models with an information theoretic approach (Burnham and Anderson 2002; Table 1). We used a natural log transformation on dependent variables that did not meet the assumption of normality and on dependent variables in certain models (i.e., dabbling ducks, diving ducks, species richness) to improve the linear relationship between dependent and independent variables (Zar 1999). For each dependent variable, we used PROC REG in SAS (SAS Institute, Inc., Cary, NC) with adjusted R^2 selection to test a global model and then to calculate Akaike's Information Criterion (AIC) for each model or subset of the model (SAS Institute, Inc. 1990). The ratio of sample size to number of parameters was small (<40), so we calculated Akaike's Information Criterion (AIC_c) scores and calculated weights, which we then used to assess models (Burnham and Anderson 2002). We determined the model with the smallest AIC_c value for each dependent variable; however, we also included models with a large relative likelihood (evidence ratio ≥ 0.37) because these models also have support from the data (Burnham and Anderson 2002). We determined the probability that any given model best explained the data by calculating the Akaike weight for each model (Burnham and Anderson 2002). We calculated the overall relative importance [$w_+(j)$] of specific habitat variables by summing the Akaike weights of all models that included the variable (Burnham and Anderson 2002). We

Table 2. Number of parameters (K), Akaike's Information Criterion (AIC_c), ΔAIC_c, and AIC_c weights (w_i) used to rank models containing factors hypothesized to predict total goose abundance in Rainwater Basin wetlands, Nebraska, USA, February–May 2002–2004. Models with smaller AIC_c and ΔAIC_c have more substantial support. Adjusted R^2 values are reported for comparison.

Yr	Model[a]	K	AIC_c	ΔAIC_c	w_i	Adj R^2
2002	AREA − WATER1	3	77.53	0.00	0.21	0.45
	AREA	2	77.60	0.06	0.21	0.43
	AREA − EMERVEG(LIN)	3	79.33	1.80	0.09	0.42
2003	AREA + WATER1 − EMERVEG(LIN) − HUNT	5	70.24	0.00	0.31	0.55
	AREA − EMERVEG(LIN) − HUNT	4	70.35	0.11	0.29	0.53
	AREA − EMERVEG(LIN) − HUNT + CROP(5)	5	72.06	1.82	0.12	0.53
2004	AREA − EMERVEG(LIN)	3	78.39	0.00	0.27	0.24
	AREA − EMERVEG(LIN) − HUNT	4	79.47	1.08	0.16	0.25
	AREA − WATER1 − EMERVEG(LIN)	4	79.51	1.12	0.16	0.25
	AREA − WATER1 − EMERVEG(LIN) − HUNT	5	80.30	1.91	0.11	0.26
All yr	AREA − WATER1 − EMERVEG(LIN) − HUNT	5	235.20	0.00	0.49	0.37

[a] Model parameters (n = 5) include mean water depth (WATER1), wetland area (AREA), linearly ranked % emergent vegetation [EMERVEG(LIN)], area of cropland within 5 km [CROP(5)], and open to hunting (HUNT).

calculated standardized regression coefficients separately for parameters in each model, and we used them to determine the relationship between predictor variables and dependent variables (Hatcher and Stepanski 1994).

RESULTS

In 2002 (17 Feb–17 May) we conducted 637 surveys and observed 945,300 migratory wetland birds representing 61 species. Wetland areas, based on the percentage of the basin that was full of water, ranged from 0.1 ha to 209.0 ha. In 2003 (16 Feb–21 May) we conducted 873 surveys and observed 517,650 birds representing 62 species. Wetland wetted areas ranged from 0.2 ha to 209.0 ha. In 2004 we conducted 955 surveys and observed 1,097,950 birds representing 64 species. Wetland areas ranged from 0.5 ha to 209.0 ha. Of the 112 total wetlands surveyed 65% were filled with snowmelt exclusively, whereas 35% were also modified by water additions by USFWS and Nebraska Game and Parks Commission (NGPC).

Wetland area influenced (+) goose abundance in best fit models for all years and the model for data pooled across years (Table 2). Hunting pressure and emergent vegetation influenced (−) abundance in best fit models for 2003 and all years combined (Table 2). Wetland area was the most important variable predicting goose abundance in 2002, 2003, and overall models; however, in 2004, percent emergent vegetation was the most important variable (Table 3). Hunting pressure was the second most important variable in models for 2003, the driest year of our study, but it had relatively less importance for models predicting goose abundance in years with more precipitation. Percent emergent vegetation consistently was an important variable in all years, whereas area of cropland within 5 km was the least important (Table 3).

Wetland area and emergent vegetation influenced (+) dabbling duck abundance in the best fit models for all years, as well as the best fit model for combined years (Table 4). Models indicate dabbling duck abundance was greatest at intermediate (50%) levels of vegetation coverage and lower at high and low levels of vegetation coverage. Dabbling duck abundance increased with area of semipermanent wetlands within 10 km for best fit models in 2002, 2003, and all years combined (Table 4). Hunting had a negative influence in alternate models from all years and the best fit overall model, whereas area of cropland within 10 km was not included in any models.

Wetland area and emergent vegetation cover were the 2 most important variables predicting dabbling duck abundance for all years (Table 3). Area of semipermanent wetlands within 10 km was similar in relative contribution to wetland area and emergent vegetation in the overall model (Table 3). Hunting pressure had a relatively greater effect on dabbling duck abundance in 2003, compared to 2002 or 2004 (Table 3), whereas area of cropland was the least important variable in all dabbling duck models.

Area and percent vegetation classified as inner marsh influenced (+) diving duck abundance in best fit models for all years, as well as in the overall model of pooled data from all years (Table 5). Water depth influenced (+) diving duck abundance in the best fit models for 2003, 2004, and all years combined. Wetland area, water depth, and percent inner marsh were all equally important in predicting diving duck abundance for all years combined (Table 3). Wetland area influenced (+) shorebird abundance in the best fit models for 2003, 2004, and all years combined, but it did not appear in the 2002 model (Table 6). Instead, the 2002 model included percent emergent vegetation and number of wetlands within 10 km as influencing (+) shorebird abundance. Wetlands with intermediate amounts of vegetation cover (25–50%) had the greatest shorebird abundance. However, 30% of sample wetlands contained <5% vegetation and 26% contained between 6% and 25% vegetation. Mean water depth, which influenced shorebird abundance (−), was present in all best fit models (Table 6). The relative importance of variables in predicting shorebird abundance varied among years. In most years, mean water depth was the most important variable in shorebird models; however, in 2003, wetland area was relatively more important than the other variables. In the overall model, local wetland variables (area, water depth, emergent vegetation) were relatively more important than landscape-scale variables (no. of wetlands within 10 km; Table 3).

Table 3. Relative importance (sum of Akaike wt over all candidate models in which the variable occurred) of habitat characteristics from regression models predicting total wetland bird abundance and species richness at Rainwater Basin wetlands, Nebraska, USA, February–May 2002–2004.

Group	Habitat variable[a]	Yr			
		2002	2003	2004	Overall
Geese	AREA	0.999	0.985	0.906	0.984
	%EMERVEG(LIN)	0.258	0.853	0.952	0.968
	WATER1	0.497	0.468	0.359	0.810
	HUNT	0.240	0.924	0.349	0.740
	CROP(5)	0.235	0.333	0.216	0.295
Dabbling ducks	AREA	1.000	0.994	0.960	0.996
	%EMERVEG(SIN)	0.714	0.994	0.949	0.996
	HUNT	0.252	0.864	0.316	0.681
	SEMIPERM(10)	0.333	0.650	0.573	0.950
	CROP(10)	0.222	0.240	0.205	0.254
Diving ducks	AREA	0.759	1.000	0.962	0.996
	%IM	0.970	0.641	0.686	0.996
	WATER2	0.307	0.701	0.949	0.996
	RIPARIAN(5)	0.218	0.366	0.475	0.252
Shorebirds	AREA	0.221	0.906	0.677	0.933
	EMERVEG(SIN)	0.965	0.526	0.286	0.912
	WATER1	0.991	0.501	0.588	1.000
	#WET(10)	0.955	0.278	0.321	0.603
Species richness	AREA	0.992	0.996	0.897	1.000
	%EMERVEG(SIN)	0.454	0.649	0.282	0.730
	WATER2	0.213	0.996	0.346	1.000
	SEMI-PERM(10)	0.919	0.996	0.531	1.000
	GRASS(5)	0.735	0.587	0.261	0.250

[a] Model parameters include wetland area (AREA), linearly ranked % emergent vegetation [EMERVEG(LIN)], mean water depth (WATER1), hunting pressure (HUNT), area of cropland within 5 km [CROP(5)], sine transformed % emergent vegetation [%EMERVEG(SIN)], area of semipermanent wetlands within 10 km [SEMIPERM(10)], area of cropland within 10 km [CROP(10)], % vegetation classified as inner marsh (%IM), max. water depth (WATER2), area of riparian habitat within 5 km [RIPARIAN(5)], no. of wetlands within 10 km [#WET(10)], and area of grassland within 5 km [GRASS(5)].

Wetland area had an influence (+) on species richness in all models for all years and the model for data pooled across years (Table 7). Area of semipermanent wetlands within 10 km influenced (−) species richness in all best fit models. Percent emergent vegetation cover (+) and water depth (−) influenced species richness in best fit models in 2003, and the overall model, indicating that species richness was greatest in shallowly inundated wetlands with intermediate vegetation coverage (Table 7). Water depth was relatively important in 2003 and the overall model, whereas area of grassland was more important in 2002 compared to other years (Table 3).

DISCUSSION

Despite similar numbers of birds wintering in the Central Flyway among years (based on the Central Flyway midwinter waterfowl survey for geese and dabbling ducks; Kruse 2005) we observed almost twice as many birds in 2002 and 2004 than in 2003. Less annual precipitation in 2003 (National Oceanic and Atmospheric Administration 2005) reduced available wetland area, shortening stopover times in the RWB, and potentially precluded birds from surveys. Due to below-average precipitation during our study, most wetlands containing water were classified as semipermanent. In addition, 85% of the 45 public wetlands that had water pumped into them were classified as semipermanent, which also contributed to the predominance of semipermanent wetlands available. Therefore, inferences drawn from our results are potentially limited to years with below average wetland availability and may not apply to migration areas or years with greater precipitation and wetland availability.

Spring hunting had the greatest effect on target (snow geese) and nontarget species (dabbling ducks) when wetland availability was least, which likely increased crowding on these wetlands that already had large densities. The similar negative response of dabbling ducks and geese to spring hunting may result in increased densities of geese and dabbling ducks on non-hunted wetlands in years of low wetland availability. Greater densities of waterfowl on RWB wetlands are thought to be positively linked to avian cholera (*Pasteurella multocida*) outbreaks (Smith and Higgins 1990); therefore, increasing goose and dabbling duck abundance on nonhunted wetlands may increase the severity of an outbreak and result in an epizootic. Because migration chronology of mallards and northern pintail partially coincides with snow goose migration and spring hunting, hunting pressure likely affected mallards and northern pintails more than other dabbling duck species.

Table 4. Number of parameters (K), Akaike's Information Criterion (AIC_c), ΔAIC_c, and AIC_c weights (w_i) used to rank models containing factors hypothesized to predict total dabbling duck abundance in Rainwater Basin wetlands, Nebraska, USA, during February–May 2002–2004. Models with lower AIC_c and ΔAIC_c have more substantial support. Adjusted R^2 values are reported for comparison.

Yr	Model[a]	K	AIC_c	ΔAIC_c	w_i	Adjusted R^2
2002	AREA + EMERVEG(SIN)	3	29.48	0.00	0.31	0.66
	AREA + EMERVEG(SIN) + SEMIPERM(10)	4	31.06	1.58	0.12	0.66
	AREA + EMERVEG(SIN) − HUNT	4	31.25	1.77	0.11	0.66
2003	AREA + EMERVEG(SIN) − HUNT + SEMIPERM(10)	5	6.73	0.00	0.43	0.72
	AREA + EMERVEG(SIN) − HUNT	4	7.81	1.08	0.25	0.69
2004	AREA + EMERVEG(SIN) + SEMIPERM(10)	4	3.83	0.00	0.46	0.47
	AREA + EMERVEG(SIN)	3	4.98	1.15	0.18	0.43
	AREA + EMERVEG(SIN) + SEMIPERM(10) − HUNT	5	5.58	1.75	0.19	0.47
All yr	AREA + EMERVEG(SIN) + SEMIPERM(10) − HUNT	5	51.27	0.00	0.48	0.62
	AREA + EMERVEG(SIN) + SEMIPERM(10)	4	52.77	1.50	0.23	0.61

[a] Model parameters (n = 5) include wetland area (AREA), area of cropland within 10 km [CROP(10)], no. of semipermanent wetlands within 10 km [#SEMIPERM(10)], sine transformed % emergent vegetation [%EMERVEG(SIN)], and hunting pressure (HUNT).

Table 5. Number of parameters (K), Akaike's Information Criterion (AIC_c), ΔAIC_c, and AIC_c weights (w_i) used to rank models containing factors hypothesized to predict total diving duck abundance in Rainwater Basin wetlands, Nebraska, USA, February–May 2002–2004. Adjusted R^2 values are reported for comparison.

Yr	Model[a]	K	AIC_c	ΔAIC_c	w_i	Adjusted R^2
2002	AREA + %IM	3	59.68	0.00	0.35	0.33
	AREA + %IM + WATER2	4	60.98	1.30	0.18	0.33
	%IM	2	61.20	1.52	0.16	0.27
2003	AREA + %IM + WATER2	4	42.85	0.00	0.26	0.50
	AREA + %IM	3	43.75	0.90	0.17	0.47
	AREA + %IM + WATER2 − RIPARIAN(5)	5	43.85	1.00	0.16	0.51
	AREA + WATER2	3	43.86	1.01	0.16	0.46
	AREA + WATER2 − RIPARIAN(5)	4	44.27	1.42	0.13	0.48
2004	AREA + %IM + WATER2 + RIPARIAN(5)	5	48.65	0.00	0.33	0.45
	AREA + %IM + WATER2	4	48.88	0.23	0.30	0.42
	AREA + WATER2	3	49.65	1.00	0.20	0.39
All yr	AREA + %IM + WATER2	4	150.69	0.00	0.72	0.38

[a] Model parameters (n = 4) include wetland area (AREA), % vegetative community classified as inner marsh (%IM), max. water depth (WATER2), and area of riparian habitat within 5 km [RIPARIAN(5)].

Geese are more likely to be disturbed by hunting during spring migration than at other times of the year, due to increased food requirements in spring for migration and breeding (Madsen and Fox 1995). The extended spring hunting season has been shown to alter or delay migration of greater snow geese (Béchet et al. 2003) and reduce body condition at staging areas (Féret et al. 2003). Although few studies have reported effects of spring hunting on nontarget species, our results indicate the spring conservation order reduces abundance of dabbling ducks on hunted wetlands and may decrease foraging opportunities (Brennan 2006), which likely combine to negatively affect dabbling ducks during migration. The long-term, nonlethal effects of hunting disturbance are difficult to quantify, because wetland birds are migratory and use a variety of habitats and behavioral strategies to complete their annual life cycle (Bell and Owen 1990). However, the extent of hunting impacts on nontarget species requires further investigation. Specifically, comparing densities, stopover time, cholera incidence, and lipid reserves of dabbling ducks on hunted and nonhunted wetlands will provide much-needed insight into the potential effects of spring hunting on dabbling ducks.

Migrating dabbling ducks in the RWB were influenced by area of wetland habitat within 10 km, reflecting the landscape-scale requirement of wetland complexes to satisfy food and shelter requirements during different life stages (Brown and Dinsmore 1986), including during migration (LaGrange and Dinsmore 1989). The relationship between dabbling duck abundance and wetland area in the landscape was most evident during times of lower wetland availability and therefore, potentially lower food availability. Dabbling ducks may be able to better meet the high energetic needs of migration by foraging in wetland complexes compared to isolated wetlands. Indeed, Smith and Sheeley (1993) reported higher fat reserves in northern pintails during wet years when birds had more access to better quality wetland habitat on wintering areas. In addition, wetland complexes containing a variety of different wetland types may provide female dabbling ducks with a greater diversity of food items compared to isolated wetlands. To meet protein demands associated with egg production, female dabbling ducks shift from a plant-dominated diet and forage more intensively on protein-rich aquatic invertebrates prior to and during egg laying (Krapu and Reinecke 1992).

Vegetation is a critical local factor influencing wetland bird use (Weller and Spatcher 1965, VanRees-Siewert and Dinsmore 1996, Davis and Smith 1998*b*, Fairbairn and Dinsmore 2001). Dense stands of emergent vegetation can

Table 6. Number of parameters (K), Akaike's Information Criterion (AIC_c), ΔAIC_c, and AIC_c weights (w_i) used to rank models containing factors hypothesized to predict total shorebird abundance in Rainwater Basin wetlands, Nebraska, USA, February–May 2002–2004. Models with lower AIC_c and ΔAIC_c have more substantial support. Adjusted R^2 values are reported for comparison.

Yr	Model[a]	K	AIC_c	ΔAIC_c	w_i	Adjusted R^2
2002	EMERVEG(SIN) − WATER1 + #WET(10)	4	13.82	0.00	0.73	0.62
2003	AREA − WATER1	3	13.79	0.00	0.19	0.28
	AREA − WATER1 + EMERVEG(SIN)	4	14.04	0.25	0.16	0.31
	AREA + EMERVEG(SIN)	3	14.15	0.36	0.16	0.27
	AREA	2	14.24	0.45	0.15	0.25
	AREA + #WET(10)	3	15.71	1.92	0.07	0.24
2004	AREA − WATER1	3	28.86	0.00	0.19	0.09
	AREA	2	29.00	0.15	0.18	0.06
	− WATER1	2	30.09	1.24	0.10	0.03
	AREA − WATER1 + #WET(10)	4	30.38	1.52	0.09	0.09
All yr	AREA − WATER1 + EMERVEG(SIN) + #WET(10)	5	55.70	0.00	0.52	0.37
	AREA − WATER1 + EMERVEG(SIN)	4	56.63	0.92	0.33	0.35

[a] Model parameters (n = 4) include wetland area (AREA), mean water depth (WATER1), sine transformed % emergent vegetation [%EMERVEG(SIN)], and no. of wetlands within 10 km [#WET(10)].

Table 7. Number of parameters (K), Akaike's Information Criterion (AIC_c), ΔAIC_c, and AIC_c weights (w_i) used to rank models containing variables hypothesized to predict total avian species richness in Rainwater Basin wetlands, Nebraska, USA, during February–May 2002–2004. Adjusted R^2 values are reported for comparison.

Yr	Model[a]	K	AIC_c	ΔAIC_c	w_i	Adjusted R^2
2002	AREA − SEMI−PERM(10) + GRASS(5)	4	130.34	0.00	0.30	0.60
	AREA + EMERVEG(SIN) − SEMI−PERM(10) + GRASS(5)	5	130.70	0.36	0.25	0.61
2003	AREA + EMERVEG(SIN) − WATER2 − SEMI−PERM(10) + GRASS(5)	6	124.86	0.00	0.37	0.70
	AREA + EMERVEG(SIN) − WATER2 − SEMI-PERM(10)	5	125.41	0.55	0.28	0.68
	AREA − WATER2 − SEMI-PERM(10) + GRASS(5)	5	125.91	1.05	0.22	0.67
2004	AREA − SEMI-PERM(10)	3	157.50	0.00	0.16	0.18
	AREA	2	157.64	0.13	0.15	0.14
	AREA + WATER2 − SEMI-PERM(10)	4	157.91	0.41	0.13	0.20
	AREA + WATER2	3	159.26	1.76	0.06	0.14
	AREA + EMERVEG(SIN) − SEMI-PERM(10)	4	159.36	1.86	0.06	0.17
	AREA SEMI-PERM(10) GRASS(5)	4	159.41	1.91	0.06	0.16
All yr	AREA + EMERVEG(SIN) − WATER2 − SEMI-PERM(10)	5	407.36	0.00	0.55	0.51

[a] Model parameters ($n = 5$) include wetland area (AREA), sine transformed % emergent vegetation [%EMERVEG(SIN)], max. water depth (WATER2), area of grassland within 5 km [GRASS(5)], and area of semipermanent wetlands within 10 km [SEMIPERM(10)].

limit feeding activity and predator detection (Metcalfe 1984, DeLeon and Smith 1999), so wetland birds often avoid wetlands with a high vegetative cover to water ratio (Weller and Fredrickson 1974, VanRees-Siewert and Dinsmore 1986). Although greater waterfowl densities and species richness at wetlands with a 50:50 ratio of open water to vegetation have been documented for breeding birds (Weller and Spatcher 1965, Weller and Fredrickson 1974, Kaminski and Prince 1984) and wintering waterfowl (Smith et al. 2004), our study demonstrates the importance of hemi-marsh conditions to dabbling ducks during migration. Hemi-marsh conditions, or equal interspersion of vegetation and open water within a wetland, provide a broad diversity of plant and macro-invertebrate food resources for waterfowl (Weller and Spatcher 1965, Kaminski and Prince 1981, Murkin et al. 1992). In addition, dabbling ducks may be using wetlands with intermediate vegetation coverage because patches of vegetation maintain pair segregation by isolating paired birds from unpaired birds (Murkin et al. 1992).

During migration, shorebirds select wetlands that offer sparse vegetation, mudflats, and shallow water, where foraging conditions are favorable (Weber and Haig 1996, Davis and Smith 1998*b*). However, we observed greater shorebird abundance on wetlands with intermediate vegetation coverage. More densely vegetated wetlands may have congregated shorebirds on limited mudflat habitat within the wetland and increased their detection compared to shorebirds that were widely dispersed across sparsely vegetated wetlands. Greater shorebird abundance in wetlands with intermediate vegetation cover also may be related to greater invertebrate density and increased foraging opportunities for migrating shorebirds. Wetlands with greater percent vegetative cover likely provide more complex habitat structure that encourages greater diversity, biomass, and density of macroinvertebrates (Nelson and Kadlec 1984, Olson et al. 1995, Kostecke et al. 2005).

Species richness increased with wetland area during migration through the RWB. Breeding bird species richness and occurrence are reported as being negatively (Fairbairn and Dinsmore 2001, Naugle et al. 2001) and positively (Brown and Dinsmore 1986) related to wetland area. Water depth and area of semipermanent wetlands within 10 km also were important variables influencing (−) species richness. Semipermanent wetlands generally are deeper than seasonal or temporary wetlands and may therefore limit species richness by precluding some species that prefer shallow foraging depths, especially shorebirds (<10 cm; Helmers 1992). Waterbird species richness and diversity often are greater at shallow water depths (Elphick and Oring 1998, Colwell and Taft 2000). Richness in our study was likely driven by shorebirds because they have the largest number of species of any of the taxonomic groups in this study. We observed more than 30 shorebird species in each year, many of which have different niches along a water depth continuum (Davis and Smith 2001). Water depth affects wetland use by shorebirds (e.g., Davis and Smith 1998*b*). Water depth was negatively correlated with shorebird abundance in all best fit models and was the most important predictor of shorebird abundance in the overall model. Deep water reduces invertebrate food resource availability for many species of migratory shorebirds (Safran et al. 1997, Isola et al. 2000, Davis and Smith 2001). Water depth was an important predictor of shorebird abundance in all years, indicating the value of semipermanent wetlands during drought years when fewer temporary or seasonal wetlands are available. Water depth had a negative influence on species richness in 2002, the midlevel precipitation year, but not in 2003 or 2004, years with the least and greatest precipitation totals, respectively. Greater precipitation, as observed in 2004, results in overall deeper wetlands that may provide habitat for some diving duck species such as red-breasted merganser (*Mergus serrator*). In addition, greater precipitation likely provides more sheet-water wetlands in agricultural fields, thereby increasing species richness in those years.

Our results elucidate several important local and landscape factors influencing habitat use by different guilds of wetland birds during migration. However, the degree to which habitat conditions on migration stopover sites influence subsequent migratory performance, body condition, breeding success, and population levels of wetland birds remains poorly understood. Before the importance of habitat quality at migration stopover sites can be understood within the context of the annual life cycle of migratory birds, its contribution should be assessed from a population-level perspective.

MANAGEMENT IMPLICATIONS

Our results demonstrate that conservation efforts should focus on wetland complexes containing a variety of different wetland types to increase dabbling duck and shorebird habitat during migration. Management activities, especially active pumping that occurs on wetlands each spring, can juxtapose wetlands within the landscape to benefit migratory waterfowl. Area, flooding regime, and water depth of wetlands within a complex should be considered when focusing on conservation of species richness during migration. Providing a diversity of wetland types will result in varying water depths within a wetland complex that likely will satisfy niche requirements for numerous wetland bird species during migration.

Given the importance of intermediate vegetative cover for dabbling duck and shorebird abundance, as well as overall species richness, efforts should be made to promote vegetation interspersion at migration stopover areas. Restoration efforts should focus on restoring the natural hydrologic conditions to wetlands, since hydroperiod is the main factor influencing plant community composition, which drives wetland trophic structure and vegetative cover patterns (Smith 1990). Alteration of RWB hydrologic conditions due to drainage and land-use practices is one of the major factors influencing wetland vegetation communities in the RWB (Gilbert 1989). Fluctuating hydroperiods allow playa wetlands to reach a productive, hemi-marsh condition. Irrigation runoff from crop fields substantially contributes to water levels in some basins (Schildman and Hurt 1984) and excavated pits in the watershed influence seasonal hydrology within RWB wetlands. Restoring hydrologic conditions will allow wetlands to cycle and promote intermediate interspersion of vegetation, ultimately enhancing habitat conditions for shorebirds and dabbling ducks while decreasing the probability that large flocks of snow geese will use the wetland.

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