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Factors Associated With Occurrence and Density of Wetland Birds in the Prairie Pothole Region of Iowa

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Wetlands within wetland complexes in northwestern, north-central, and central Iowa were surveyed for bird use in 1997 and 1998. Species occurrence, species richness, and density of nesting species were related to wetland habitat variables. A habitat diversity index measuring the evenness of distribution of the different habitats within a wetland was the best predictor of species richness in both years. The habitat diversity index was also the best predictor of the occurrence of individual species in both 1997 and 1998. Eight of 11 species (73%) in 1997 and 13 of 18 species (72%) in 1998 had greater densities in smaller wetlands. The probability of occurrence and density of individual species also were related to one or more other variables, such as the percent of the wetland that was covered by the different vegetation zones. Most species were more likely to be present and in greater abundance in wetlands that contained more of their preferred nesting habitat. Wetland restoration priorities should emphasize restoring groups of wetlands of a variety of sizes and types to attract the greatest diversity of wetland species as well as greater densities of individual species. If a species is of management concern, those factors that are associated with a greater probability of occurrence and/or a greater density should be considered when selecting sites to restore to wetland conditions.

INDEX DESCRIPTORS: wetlands, wetland birds, wetland restoration, wetland ecology, restoration ecology, waterfowl, wetland management, Iowa.

Since about 1850, about 90% of Iowa's wetland habitat has been lost (Dahl 1990). The loss has been most severe in the Prairie Pothole Region of north-central and northwestern Iowa, where approximately 99% of the wetlands have been lost (Bishop et al. 1998), primarily to drainage for agricultural purposes. However, in the past decade, several federal programs have worked to restore some of that land to wetland conditions. Since 1988, more than 3,650 wetland hectares in Iowa have been restored through the Prairie Pothole Joint Venture of the North American Waterfowl Management Plan (Zohrer 1999). Additionally, more than 31,500 hectares are currently under contract to be restored by the Wetland Reserve Program of the Natural Resources Conservation Service and about 2,400 hectares by Partners for Wildlife.

These restoration efforts are known to be important in providing habitat for wetland-dependent birds (Hemesath and Dinsmore 1993, VanRees-Siewert and Dinsmore 1996). Both the amount and the type of vegetation within a wetland are important in determining the probability of occurrence of individual species (Weller and Spatcher 1965, Naugle 1997). This paper investigates how habitat factors affect both bird species occurrence and density in individual wetlands, and which variables are important predictors of wetland bird-species richness.

METHODS

Study Sites

Study sites consisted of 74 wetlands in 1997 and 151 wetlands in 1998. The wetlands were all within wetland complexes, which were defined as tracts of land containing multiple wetlands within a matrix of upland habitats covered predominantly by smooth brome (*Bromus inermis*) or switchgrass (*Panicum virgatum*). All wetlands were in the Prairie Pothole Region in central, north-central, and northwestern Iowa (see Fairbairn 1999 for more details). Wetlands ranged from 0.04 ha to 20.5 ha with a mean of 2.2 ha. The water regime of these wetlands ranged from ephemeral wetlands that contain water briefly following a precipitation event to semipermanent wetlands that contain water throughout most years (see Stewart and Kantrud 1971). Thirty-three restored and 41 natural wetlands were studied in 1997, and 115 restored and 36 natural wetlands were studied in 1998. Upland and wetland management practices were similar on all sites.

Bird Surveys

We surveyed birds on each wetland once yearly to determine the species richness and the number of individuals of each species that were present in each wetland. Surveys were conducted from mid-May through the first week in July between dawn and approximately 4 hr post-dawn. Due to the variety of species and wetland habitats present, several survey methods were used. Prior to entering a wetland, any open water present was observed from a vantage point, and all birds seen on the open water were recorded. Tape recordings of the calls of four secretive wetland bird species [Virginia Rail (see Table 1 for scientific names), Sora, American Bittern, and Least Bittern] were played at a set of predetermined points. The number of points selected per wetland was determined using the following criteria: one point in wetlands up to 0.4 ha, two points for those between 0.4 and 1.0 ha, three points for 1.0 to 2.0 ha wetlands, and one point was added for each additional 1.6 ha. Each point was visited for 6 minutes, with taped calls of the four secretive species played during the middle two minutes. This method has been shown to be effective in evoking responses from these species (Gibbs and

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Table 1. Wetland bird species and the number of wetlands in which they nested in the Prairie Pothole Region of Iowa in 1997 and 1998. A total of 74 wetlands were surveyed in 1997 and 151 in 1990.

Species	Percentage of wetlands where species nested	
	1997	1998
Pied-billed Grebe (*Podilymbus podiceps*)	14.9	25.2
Red-necked Grebe (*Podiceps grisegena*)	0	0.7
American Bittern (*Botaurus lentiginosus*)	1.4	2.0
Least Bittern (*Ixobrychus exilis*)	2.7	13.2
Canada Goose (*Branta canadensis*)	36.5	31.8
Wood Duck (*Aix sponsa*)	20.3	34.4
Gadwall (*Anas strepera*)	4.1	15.9
Mallard (*Anas platyrhynchos*)	39.2	66.9
Blue-winged Teal (*Anas discors*)	52.7	69.5
Northern Pintail (*Anas acuta*)	1.4	2.0
Redhead (*Aythya americana*)	0	0.7
Ruddy Duck (*Oxyura jamaicensis*)	0	4.6
Virginia Rail (*Rallus limicola*)	27.0	20.5
Sora (*Porzana carolina*)	2.7	14.6
American Coot (*Fulica americana*)	13.5	29.8
Killdeer (*Charadrius vociferus*)	4.1	2.6
Forster's Tern (*Sterna forsteri*)	0	1.3
Black Tern (*Chlidonias niger*)	0	2.0
Willow Flycatcher (*Empidonax traillii*)	13.5	6.6
Sedge Wren (*Cistothorus platensis*)	25.7	38.4
Marsh Wren (*Cistothorus palustris*)	37.8	23.2
Common Yellowthroat (*Geothlypis trichas*)	66.2	70.2
Swamp Sparrow (*Melospiza georgiana*)	60.8	55.6
Red-winged Blackbird (*Agelaius phoeniceus*)	100.0	98.0
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	44.6	30.5
Common Grackle (*Quiscalus quiscula*)	48.6	32.5
Great-tailed Grackle (*Quiscalus mexicanus*)	0	5.3

Melvin 1997). As the observer waded through the emergent vegetation between points, all birds that were seen or heard were noted. Singing males were assumed to have one mate in the same wetland and were counted as two individuals unless a female of that species was observed nearby. In that case, the female was assumed to be the mate and each bird was recorded as one individual. Waterfowl were counted following the protocol of the U.S. Fish and Wildlife Service's spring pair counts (U.S. Fish and Wildlife Service 1987).

For each wetland, each species was assigned a breeding status, based on the probability that the species nested within the wetland. A species was considered a confirmed breeder if young, eggs, or a nest were found; a probable breeder if its behavior was consistent with nesting and there was a considerable amount of suitable nesting habitat available; or a possible breeder if it was observed in a wetland with either little suitable habitat or with marginal nesting habitat. A final category, casual users, included species that do not normally nest in wetlands but were using this habitat for other reasons such as feeding or resting. Densities of confirmed or probable breeders within a wetland were calculated by dividing the total number of individuals of a species by the area of the wetland.

Vegetation

All vegetation sampling was done between 7 and 17 July in both years. The vegetation zones described by Stewart and Kantrud (1971) were mapped using a modification of the releve method (Mueller-Dombois and Ellenberg 1974, Galatowitsch and van der Valk 1993). Low-prairie and wet-meadow zones were combined because of the similarity in their vegetative structure. The width of each zone was measured at 15- to 20-m intervals or where obvious changes in the width occurred. The percent coverages of individual plant species within these zones were estimated visually, and each species covering > 5% of a zone was recorded. Within zones, plant species were grouped into robust- and weak-stemmed categories following Weller and Spatcher (1965) and Kantrud et al. (1989).

Aerial farm compliance photos for each study site were obtained from the Farm Service Agency (USDA). Maps of each wetland were digitized directly from the slides, and their area and perimeter were measured using ArcView (Environmental Systems Research Institute, Redlands, CA). ArcView also was used to calculate the area of the vegetation zones within a wetland and the percentage of the wetland that each zone covered.

A habitat diversity index (HABDIV) was calculated with the following formula: $-\Sigma p_i * (\ln p_i)$, where p_i is the proportion of the wetland area within a wetland that consists of habitat i. This index, a modification of the Shannon-Wiener diversity index, is a measure of the evenness of the distribution of the various wetland habitats (Magurran 1984). A perimeter-to-area index (PAINDEX) also was calculated as an indicator of the relative amount of wetland shoreline in each wetland. The formula used was: perimeter/$\{2 (\text{area} * \Pi)^{1/2}\}$. As the shape of a wetland deviates from a circle, PAINDEX increases from one (Patton 1975).

Data Analysis

Data analyses were performed only for those species that were considered confirmed or probable breeders (Table 1). A total of 22 explanatory variables were identified (Table 2). A correlation analysis

Table 2. Description of variables that were measured to evaluate bird use of wetlands in the Prairie Pothole Region of Iowa in 1997 and 1998.

Variable	Description
AREA[a]	area of the wetland (m^2)
EMERG%[a]	percentage of wetland area that is covered with emergent vegetation
WETMEADOW%[a]	percentage of wetland area that is covered with wet-meadow vegetation
WATER%[a]	percentage of wetland area that is covered with open water
MUDFLAT%[a]	percentage of wetland area that is mudflat habitat
PAINDEX[a]	perimeter-to-area index that increases from 1 as a wetland's shape deviates from a circle (see methods for formula)
RESNAT[a]	categorical variable; restored wetland = 0 and natural wetland = 1
HABDIV[a]	habitat diversity index that measures the evenness of distribution of the vegetation zones (see methods for formula)
EMROBUST[b]	area of robust emergent vegetation cover (m^2)
WMWEAK[b]	area of weak-stemmed wet-meadow vegetation cover (m^2)
EMOPEN[b]	area of open water within emergent zones (m^2)
EMWEAK[c]	area of weak-stemmed emergent vegetation cover (m^2)
EMWOOD[c]	area of woody-emergent vegetation cover (m^2)
WMROBUST[c]	area of robust wet-meadow vegetation cover (m^2)
WMBARE[c]	area of bare ground within the wet-meadow zone (m^2)
WMWOOD[c]	area of woody wet-meadow vegetation cover (m^2)
MFBARE[c]	area of unvegetated mudflat (m^2)
MFVEG[c]	area of mudflat covered with vegetation (m^2)
EMAREA[c]	total area of the emergent-vegetation zone (m^2)
WMAREA[c]	total area of the wet-meadow vegetation zone (m^2)
OWAREA[c]	total area of open water (m^2)
MFAREA[c]	total area of the mudflat zone (m^2)

[a]Variables that were included in the selection procedure for all models.
[b]Variables that were included in the selection procedures for a limited number of models.
[c]Variables that were measured but not used in the selection procedure for any of the models.

was performed on these variables, and 14 that were highly correlated ($r > 0.5$) with other variables were eliminated. This reduced the number of variables that were included in subsequent analyses to eight (Table 2). Multiple stepwise logistic regressions were used to determine which variables were the most important predictors of species occurrences. Wetland area was included in all models prior to the stepwise regressions to adjust for differences in wetland size and thus differences in sampling effort. The other eight variables then entered the model if they added significantly ($P < 0.05$) to the probability of occurrence of a species as determined from Wald's chi-square statistic (Cody and Smith 1997).

Next, those variables that were associated with changes in species densities were identified. Wetlands that did not contain a species were not included in the multiple regressions for that species. The same eight variables that were used in the logistic regression models were used in the linear regression models (Table 2). Additionally, for some species, other variables were included in the regressions to test whether they significantly added information to the model. These additional variables were included based on their previously documented biological importance for that particular species and because the variables with which they were correlated were not selected for inclusion in the linear regression model (Table 2). For example, if the density of a species that nests in emergent vegetation was not associated with EMERG%, then other variables related to the emergent-vegetation zone were tested to see if they were selected for inclusion in the model. The set of all possible models for each species was generated using the RSQUARE option in PROC REG of SAS (SAS Institute 1990), and the best overall model was selected based on Schwarz's Bayesian Criterion (SBC) (Schwarz 1978). The final models were then evaluated for correlations of species densities among wetlands within complexes. This was done by comparing log likelihoods of mixed models (PROC MIXED; SAS), which allow for correlation of species densities among wetlands within a complex, and models that assumed independence of wetlands. The difference in the two log likelihoods approximates a chi-squared distribution with one degree of freedom. Based on this test, none of the models allowing for covariance among wetlands was different from fitting the null model that assumed independence of densities among wetlands ($P > 0.05$). Thus, the variable coefficients were generated under the assumption of independence of wetlands using a multiple linear regression.

RESULTS

Species-Occurrence Models

Twenty-two species of wetland birds were identified as breeding in the 74 wetlands surveyed in 1997, and 28 species were found breeding in the 151 wetlands in 1998 (Table 1). No variables were selected for inclusion in an occurrence model for eight species in 1997 and for three species in 1998. For all but one species, this was due to the limited number of wetlands where these species were found. The other case was the Red-winged Blackbird in 1997, which was found in all 74 wetlands that were surveyed that year. After the models were adjusted for AREA, HABDIV was the most frequently selected variable for predicting the occurrence of wetland bird species in 1997 and 1998 (Table 3). HABDIV was positively associated with 5 of 14 (36%) species in 1997 and 9 of 25 (36%) in 1998.

In 1997, after HABDIV, the next most frequently selected variables were RESNAT, WETMEADOW%, and MUDFLAT%; each was associated with the occurrence of three species (Table 3). Canada Goose, Virginia Rail, and Swamp Sparrow were more likely to be present in natural than restored wetlands. The probability of occurrence of Sedge Wren was positively related to the percentage of the wetland that was covered by wet-meadow vegetation, whereas Canada Goose and Common Yellowthroat were negatively related to WETMEADOW%. Three species, Marsh Wren, Common Yellowthroat, and Swamp Sparrow, were all negatively related to the percentage of the wetland that was mudflat habitat.

The occurrence of two species was significantly predicted by the perimeter-to-area index, PAINDEX (Table 3). The occurrence of

Table 3. Models relating wetland bird species occurrences to habitat variables in wetlands in the Prairie Pothole Region of Iowa in 1997 and 1998. See Table 1 for scientific names of species and Table 2 for variable abbreviations and definitions. AREA was included in all models, and the other variables are listed in the order in which they were selected for inclusion in the regression models.

Species	Year	Intercept +/− (coefficient) variables included in the model
Pied-billed Grebe	1997	−9.87 + (0.00002)AREA + (7.85)HABDIV
	1998	−3.95 + (0.00004)AREA + (1.87)EMERG% + (1.95)HABDIV
American Bittern	1998	−15.7 + (0.00005)AREA + (8.95)PAINDEX
Least Bittern	1998	−7.94 + (0.00004)AREA + (4.71)EMERG% + (4.22)HABDIV
Canada Goose	1997	−1.13 + (0.00007)AREA + (2.28)RESNAT − (4.54)WETMEADOW%
	1998	−2.70 + (0.00005)AREA + (1.71)WATER%
Wood Duck	1997	−13.9 + (0.00009)AREA + (10.3)HABDIV
	1998	−3.22 + (0.00006)AREA + (2.01)HABDIV
Gadwall	1998	−3.37 + (0.00002)AREA + (2.17)WATER%
Mallard	1997	3.14 + (0.00001)AREA − (4.63)PAINDEX
	1998	−1.04 + (0.00006)AREA + (2.42)WATER%
Blue-winged Teal	1997	−3.23 + (0.00006)AREA + (2.78)HABDIV
	1998	0.628 + (0.00005)AREA − (1.28)WETMEADOW%
Northern Shoveler	1998	−1.11 + (0.00002)AREA − (5.94)WETMEADOW%
Northern Pintail	1998	−4.83 + (0.00002)AREA
Ruddy Duck	1998	−4.23 + (0.00003)AREA
Virginia Rail	1997	−2.07 + (0.00002)AREA + (1.24)RESNAT
	1998	−3.03 + (0.00004)AREA − (3.39)WATER% + (2.84)HABDIV
Sora	1998	−2.12 + (0.00001)AREA
American Coot	1997	−3.66 + (0.00002)AREA + (4.78)EMERG%
	1998	−2.60 + (0.00002)AREA + (1.66)HABDIV
Forster's Tern	1998	−5.38 + (0.00002)AREA
Black Tern	1998	−5.37 + (0.00003)AREA
Willow Flycatcher	1997	−6.73 + (0.0000004)AREA + (3.33)PAINDEX
	1998	−3.42 + (0.00001)AREA + (1.64)RESNAT
Sedge Wren	1997	−3.69 + (0.00005)AREA + (3.08)WETMEADOW%
	1998	−1.68 + (0.00003)AREA + (1.54)WETMEADOW%
Marsh Wren	1997	−15.0 + (0.0003)AREA − (93.4)MUDFLAT% − (12.7)WATER% + (15.4)HABDIV
	1998	−3.36 + (0.00005)AREA − (3.14)WATER% + (2.95)HABDIV
Common Yellowthroat	1997	+2.99 + (0.00003)AREA − (28.6)MUDFLAT% − (3.69)WETMEADOW%
	1998	0.130 + (0.0001)AREA − (2.86)PAINDEX + (3.14)WETMEADOW% + (2.23)HABDIV
Swamp Sparrow	1997	−0.380 + (0.00005)AREA + (1.62)RESNAT − (22.0)MUDFLAT%
	1998	−2.74 + (0.00005)AREA + (1.76)WETMEADOW% + (2.17)HABDIV
Red-winged Blackbird	1998	+3.93 + (0.00068)AREA − (6.27)WATER%
Yellow-headed Blackbird	1997	−9.53 + (0.00009)AREA + (8.28)HABDIV
	1998	−3.61 + (0.000003)AREA + (2.86)EMERG% + (1.84)HABDIV
Common Grackle	1998	−1.78 + (0.00005)AREA
Great-tailed Grackle	1998	−4.38 + (0.000006)AREA + (4.18)EMERG%

Mallard was negatively related to PAINDEX, whereas the occurrence of Willow Flycatcher was positively related to this index. The occurrence of two species was predicted by the percentage of open water in the wetland. The occurrence of Marsh Wren was negatively related to WATER%, whereas Common Grackle occurrence was positively related to this variable. The occurrence of American Coot was positively related to the percent of the wetland that was covered by emergent vegetation.

In 1998, after HABDIV, the next most important habitat variable was WATER%, which was a significant predictor of the occurrence of six species. Canada Goose, Gadwall, and Mallard were positively associated with WATER%. Virginia Rail, Marsh Wren, and Red-winged Blackbird were negatively associated with WATER%. WETMEADOW% was a significant predictor of the occurrence of five species. Sedge Wren, Common Yellowthroat, and Swamp Sparrow were positively associated with the percentage of wet-meadow vegetation in the wetland, whereas Blue-winged Teal and Northern Shoveler were negatively associated with wet-meadow coverage. Four species—Pied-billed Grebe, Least Bittern, Yellow-headed Blackbird, and Great-tailed Grackle—were positively related to the percentage of emergent vegetation within the wetland (Table 3). No species was negatively related to this variable. American Bittern was positively related to PAINDEX, and Common Yellowthroat was negatively associated with this index. The Willow Flycatcher was positively related to RESNAT.

Species Richness Models

AREA was included in the regression models for species richness within wetlands in 1997 and 1998. In 1997, species richness was

Table 4. Models relating to wetland bird species densities to habitat variables in wetlands in the Prairie Pothole Region of Iowa in 1997 and 1998. See Table 1 for scientific names of species and Table 2 for variable abbreviations and definitions. Variables are listed in the order in which they were selected for inclusion in the regression models.

Species	Year	Intercept +/− (regression coefficients) variables included in the model	r^2	P-value
Species richness	1997	−0.733 + (0.00005)AREA + (1.05)RESNAT + (1.83)PAINDEX + (3.25)WATER% + (2.68)HABDIV	0.68	0.0001
	1998	3.11 + (0.00008)AREA + (0.00002)EMROBUST + (2.93)HABDIV	0.58	0.0001
Pied-billed Grebe	1998	0.875 − (0.000007)AREA + (0.819)WETMEADOW%	0.40	0.0001
Least Bittern	1998	0.795 − (0.000005)AREA	0.38	0.004
Canada Goose	1997	2.15 + (0.000005)AREA − (2.00)WETMEADOW% − (1.47)HABDIV	0.76	0.0001
	1990	8.58 − (4.59)PAINDEX	0.09	0.034
Wood Duck	1998	34.7 − (17.1)PAINDEX − (0.0001)AREA	0.07	0.167
Gadwall	1998	6.08 − (0.00007)AREA − (3.39)WATER% − (3.34)HABDIV	0.61	0.0002
Mallard	1997	2.27 − (0.00002)AREA + (11.8)MUDFLAT%	0.25	0.026
	1998	14.8 − (0.00017)AREA	0.05	0.033
Blue-winged Teal	1997	7.21 − (0.00003)AREA − (3.85)HABDIV	0.31	0.001
	1998	6.47 − (0.00006)AREA	0.11	0.0006
Northern Shoveler	1998	4.45 − (0.00004)AREA	0.22	0.037
Virginia Rail	1997	1.44 − (0.00002)AREA + (0.00015)EMOPEN	0.40	0.013
	1998	0.940 − (0.000009)AREA + (0.824)EMERG%	0.34	0.003
Sora	1998	3.30 − (0.00006)AREA + (0.00007)EMOPEN	0.35	0.018
American Coot	1998	3.69 − (1.90)RESNAT − (0.00002)AREA	0.14	0.046
Sedge Wren	1997	16.6 − (15.6)HABDIV	0.33	0.010
	1998	−0.243 + (11.6)WETMEADOW%	0.31	0.0001
Marsh Wren	1997	2.07 + (1.57)RESNAT − (0.00001)AREA	0.36	0.004
	1998	−1.68 + (4.64)WETMEADOW% + (3.54)HABDIV	0.29	0.004
Common Yellowthroat	1997	9.70 − (14.1)WATER%	0.18	0.003
	1998	3.24 − (0.00004)AREA + (6.35)WETMEADOW%	0.31	0.0001
Swamp Sparrow	1997	1.04 − (0.00004)AREA + (9.56)WETMEADOW%	0.35	0.0001
	1998	3.60 − (0.00005)AREA + (5.05)WETMEADOW%	0.18	0.0003
Red-winged Blackbird	1997	7.82 − (0.00009)AREA + (8.18)WETMEADOW%	0.15	0.003
	1998	17.6 − (0.00023)AREA − (11.1)WATER% + (0.00015)WMWEAK	0.26	0.0001
Yellow-headed Blackbird	1997	0.340 + (10.8)EMERG% + (17.7)MUDFLAT%	0.29	0.006
	1998	10.0 − (10.2)WATER%	0.35	0.0001
Common Grackle	1997	2.63 − (0.00002)AREA	0.03	0.280
	1998	0.160 + (4.75)WETMEADOW%	0.15	0.007

positively related to RESNAT, PAINDEX, WATER%, and HABDIV (Table 4). In 1998, with AREA already in the model, species richness had a positive association with EMROBUST and HABDIV (Table 4).

Species Density Models

AREA was selected for inclusion in models for 8 of the 11 (73%) species for which models predicting density were created in 1997 (Table 4). For seven of these species, densities were negatively related to the wetland area, whereas Canada Goose density showed a positive relationship with wetland area. WETMEADOW% and HABDIV were each included in density models for three species. Swamp Sparrow and Red-winged Blackbird densities were positively related to the percentage of the wetland that was covered by wet-meadow vegetation, whereas Canada Goose density was negatively related with this variable. Canada Goose, Blue-winged Teal, and Sedge Wren densities were negatively related to the habitat diversity index.

In 1998, 12 of the 17 (71%) species density models were negatively associated with AREA (Table 4). The densities of six species (Pied-billed Grebe, Sedge Wren, Marsh Wren, Common Yellowthroat, Swamp Sparrow, and Common Grackle) were positively associated with WETMEADOW%. Gadwall, Red-winged Blackbird, and Yellow-headed Blackbird densities were negatively associated with WATER%. Canada Goose density was negatively related to the PAINDEX. Marsh Wren densities were positively related with the HABDIV, whereas Gadwall density was negatively associated with this index. Densities of two rail species were positively related to an emergent vegetation zone variable. Sora densities were related to EMOPEN, and Virginia Rail densities were related to EMERG%. The density of the American Coot was less in natural wetlands than it was in restored wetlands.

DISCUSSION

Species Richness and Occurrence Models

A habitat diversity index, which was based on the evenness of distribution of the various habitats within a wetland, was the most frequently selected variable in predicting the occurrence of individual species. This type of index has been discussed as a measure of available niches (Magurran 1984). That species richness increases as this index increases suggests that the index may be a good predictor of the number of species that a particular wetland is capable of supporting. One explanation for the probability of occurrence of so many species being related to this diversity index is that many of these species require more than one type of habitat within a wetland for different parts of their life histories. For example, Pied-billed Grebes require emergent vegetation for nesting and open water for courtship behavior, feeding, and loafing. Wetlands that have greater values for the habitat diversity index are more likely to have coverages of both habitat types needed by Pied-billed Grebes.

Most of the other variables that were examined are directly related to a specific habitat type within a wetland. So in order to increase the probability of occurrence of particular species, the variables included in the logistic regression models should be considered (Table 3). Most of the variables selected for the models make intuitive sense. For example, considering only the 1998 data, the occurrence of three species that are most commonly considered as wet-meadow or low-prairie species (Sedge Wren, Common Yellowthroat, and Swamp Sparrow) were all positively associated with the percentage of the wetland that was covered by wet-meadow vegetation (Table 3). Pied-billed Grebe, Least Bittern, Yellow-headed Blackbird, and Great-tailed Grackle occurrences were all positively associated with the percentage of the wetland that was covered by emergent vegetation. All of these species nest in this vegetation zone and/or use emergent vegetation for their nest substrate. Two other species (Virginia Rail and Marsh Wren) that are commonly associated with emergent vegetation were negatively related to the percentage of the wetland that is comprised of open water. The occurrences of three waterfowl species (Canada Goose, Gadwall, and Mallard) were positively related to the percentage of open water in the wetland, whereas two others (Blue-winged Teal and Northern Shoveler) had a negative relationship with the percentage of wet-meadow vegetation within the wetland.

Species Density Models

AREA was the most commonly selected variable to explain variation in species densities. However, in all but one case (Canada Goose in 1997), the density of the species was negatively related to wetland area. One explanation for this is that smaller wetlands tend to have a greater proportion of vegetative cover than larger wetlands. Because the densities were calculated by dividing the abundance of a species by the total wetland area, these smaller wetlands tend to have a greater proportion of their surface covered by suitable habitat and hence are able to support higher densities of birds. Waterfowl probably show a negative association with wetland area because even the smallest potholes that were studied had at least one pair of ducks. So when comparing densities, these small wetlands with one pair have greater densities than larger wetlands with several pairs.

When specific habitat variables are considered, the densities of various species often increase in association with an increase in the percentage of the wetland that is comprised of a particular habitat type. The fact that Marsh Wren, Sedge Wren, Common Yellowthroat, Swamp Sparrow, and Common Grackle densities all increase with an increase in the percentage of wet-meadow vegetation indicates that these species may be selecting the wetland in which to nest based on its vegetation structure.

Management Implications

Our models suggest that each species has particular habitat requirements that must be met for the species to be present in a wetland. This indicates that with the current emphasis on wetland restoration, future efforts need to focus on restoring complexes of wetlands with a variety of water regimes. By doing so, we improve the chances of restoring the hydrology to best resemble the original hydrology of the area (Galatowitsch and van der Valk 1996). Restoring wetlands within complexes also insures that a greater variety of vegetative communities are available for the diverse needs of the members of this avian community. Restoring different wetland types and sizes in a complex is important both for increased probability of occurrence of different bird species, and also is important for increased densities of various species. Densities of many wetland bird species are greater in smaller wetlands, indicating that these smaller, usually less permanent, wetlands are possibly more important than larger, more permanent, wetlands for some species. By restoring all wetland basins within a tract of land, we have the best chance of recreating an area that most closely resembles the landscape before the wetlands were drained. This should provide an adequate variety of habitats for most of the wildlife species that were present in these wetlands prior to drainage.

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