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DABBLING DUCK-HABITAT ASSOCIATIONS DURING SPRING IN DELTA MARSH, MANITOBA¹

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Abstract: We conducted helicopter surveys of dabbling ducks (Anatini) in randomly selected legal quarter sections (64.8 ha) in the Delta Marsh, Manitoba, between April and June 1976-78. Our objective was to census indicated pairs of five species (*Anas acuta*, *A. clypeata*, *A. discors*, *A. platyrhynchos*, *A. strepera*) to test for associations of species pair densities and species richness with floristic and physiognomic characteristics of surveyed areas. Water levels in Delta Marsh varied markedly among years with 1976, 1977, and 1978 representing high, low, and intermediate levels, respectively. Densities of most species increased dramatically in 1977, a year of widespread drought. We suggest this resulted from influxes of dabblers displaced from drought-stricken habitats. Tests for dabbler-habitat correlations with stepwise multiple regression revealed several patterns. Pair densities of most species and species richness were positively correlated with the proportional cover of shallow marsh habitat within survey quarters in 1976, but negatively associated with the cover of forest in 1977. Only mallard, northern pintail, and species richness were positively associated with an index of emergent vegetation-water interspersion in all 3 years. We provide explanations for consistent habitat correlations and offer considerations for marsh management and future research.

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Most species of North American waterfowl use a variety of habitats annually due to their migratory nature, their seasonally changing physiological needs, and fluctuations in resource availability (Weller 1974, Flake 1978). Generally, birds are attracted to habitats by "proximate" cues that perhaps reflect the presence of certain "ultimate" elements necessary for survival and/or reproduction (Hilden 1965). Anderson (1979) and Wiens and Rotenberry (1981b) cited a number of studies indicating that habitat physiognomy (i.e., physical structure) correlates with occupancy, abundance, diversity, and community organization of terrestrial bird species. Similar relationships have been documented for waterfowl (e.g., Weller and Spatcher 1965, Weller and Fredrickson 1973, Courcelles and Bédard 1979).

Recent advances in user-oriented multiple regression and different multivariate procedures have greatly increased their application in avian habitat studies (Capen 1981, Wiens and Rotenberry 1981a). Among the many waterfowl habitat studies, a number of investigators have used such procedures to discern patterns in habitat use by breeding ducks and/or broods mainly in pothole habitats (e.g., Trauger 1967, Mulhern 1982, Nudds 1983) and man-made wetlands (e.g., Lokemoen 1973, Flake et al. 1977, Mack and Flake 1980). However, we are unaware of any studies taking a similar approach to elucidate habitat correlations of breeding ducks in large prairie marshes. Here, we focus on spring habitat associations of five dabbling duck species (mallard, blue-winged teal, northern shoveler, gadwall, northern pintail) in the Delta Marsh, Manitoba, as revealed by stepwise multiple regression. We examined four questions. (1) Are indicated pair densities of dabbling ducks and species richness (i.e., number of dabbling duck species) correlated with floristic and physiognomic

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characteristics of the Delta Marsh? (We predicted that both would correlate positively with indices of habitat structural diversity and assumed that yearly variation in number of pairs and species would reflect current occupancy potential of sampled habitats.) (2) Do species pair densities and species richness correlate with the same habitat variables? (3) Do patterns in habitat association (or their absence) occur across species within and among years? (4) What practical implications can be derived from any such relationships?

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STUDY AREA

The 180-km² Delta Marsh in south-central Manitoba (50°11'N, 98°19'W) is a complex of meadows, potholes, bays, and channels contiguous with the forested beach ridge south shore of Lake Manitoba (Hochbaum 1944). Our study was confined to the east marsh unit (ca. 105 km²) between the villages of Delta and St. Ambrose. Descriptions of the local flora (Love and Love 1954, Anderson and Jones 1976,

MacKenzie 1982) and physiography (Elson 1967, Fenton 1970) are available.

METHODS

Breeding Pair Surveys

Using a map of the marsh with delineated legal quarter sections (64.8 ha), we randomly selected 50 quarters from a universe of 135 to serve as census units for indicated pairs of dabbling ducks (i.e., pairs plus lone males) in 1976 and 1977. The sample population included all quarters that contained some visible open water on 1969 aerial photographs. The cover of visible open water on these photos was similar to that appearing on 1977 color-infrared imagery of the Delta Marsh. In 1978, we reduced sampling effort by randomly selecting and surveying 20 of the original 50 quarters.

We censused indicated pairs (henceforth referred to as pairs) from a Bell 47G4A helicopter at 10–18-day intervals ($\bar{x} = 14$). One observer (R.M.K.) conducted all surveys; six in 1976 (12 Apr–21 Jun), five in 1977 (18 Apr–16 Jun), and three in 1978 (28 Apr–29 May). Surveys were conducted between 0730 and 1345 hours, but 12 of 14 were completed before 1200 hours. Approximately 4 hours were needed to survey 50 quarters. All surveys were conducted under similar weather conditions (i.e., predominantly clear, winds <30 km/hour, no precipitation).

During surveys, quarters were located by comparing conspicuous landscape features between the ground and aerial photographs. After locating each quarter from high altitudes, we descended to approximately 30 m for censusing. Four passes were usually required to survey a quarter. Approximate locations of pairs were marked on a plastic overlay of the aerial photographs.

Habitat Measurements and Data Analyses

Surveyed quarters were divided into four subunits (16.2 ha) on the aerial photographs for habitat measurements and statistical analyses. For each survey, one of the four subunits was randomly selected and these were pooled by year for statistical analyses. This procedure enabled examination of dabbler-habitat associations on a more detailed scale and established independence among subunits. Using 1977 color-infrared imagery of the Delta Marsh supplemented with ground reconnaissance, we mapped and then estimated (with a dot grid) the proportional cover of the dominant habitats within each subunit: (1) open water, (2) forest, (3) common reed (*Phragmites communis*), (4) whitetop rivergrass (*Scolochloa festucacea*)-awned sedge (*Carex atherodes*), and (5) cattail (*Typha* spp.)-tule bulrush (*Scirpus acutus*). Whitetop rivergrass and awned sedge were combined, as were cattail and tule bulrush because of life-form similarities and frequent co-occurrence. The number of different emergent plant communities per subunit was used to index emergent habitat richness. We computed shoreline development (Reid 1961) by dividing each subunit's total length of emergent vegetation-water interface by $2\sqrt{\pi \cdot A}$, where A = area of open water within each subunit. In addition, we indexed the extent of vegetation-water interspersions by counting the number of times a diagonal line (connecting the northwest and southeast corners of subunits) intersected a vegetation-water interface. Plant community edge was indexed similarly by tallying the number of times the diagonal crossed an apparent edge between two distinct plant communities. Within-year temporal variation in

species pair densities and richness was accounted for by including survey number as a variable in our analyses.

We used simple correlation analysis to determine if the measured habitat variables were intercorrelated before testing for associations with species pair densities and species richness with stepwise multiple regression (Helwig and Council 1979). Kim and Kohout (1975:341) cautioned that excessive multicollinearity (i.e., $r > 0.8$) can cause operational and interpretive problems. They suggested that a possible solution is to use only one variable of an interrelated set of variables. We established a priori that only one variable of an interrelated ($r \geq 0.7$) set of variables would be subjected to multiple regression analysis. Emergent habitat richness was positively correlated ($0.72 \leq r \leq 0.83$) with plant community edge and negatively correlated ($-0.75 \leq r \leq -0.81$) with open water in each year's data set. Because emergent habitat richness correlated with both other variables and it intuitively related to the dependent variables in a straightforward manner, we retained it for multiple regression analysis but deleted the other two variables. Species pair density and richness data were transformed ($\sqrt{x + 0.5}$) because zero values occurred (Zar 1974:220). We gauged the strength of association between dependent variables and explanatory variables retained ($P \leq 0.1$) in the stepwise process by the coefficient of multiple correlation (R), an appropriate statistic for demonstrating association rather than predictive precision (Gill 1978:312). The relative influence of explanatory variables on the dependent variables was indexed by the absolute value of the formers' standardized regression coefficients (Kim and Kohout 1975:332).

We did not analyze census data that seemed biased by perturbations unrelated

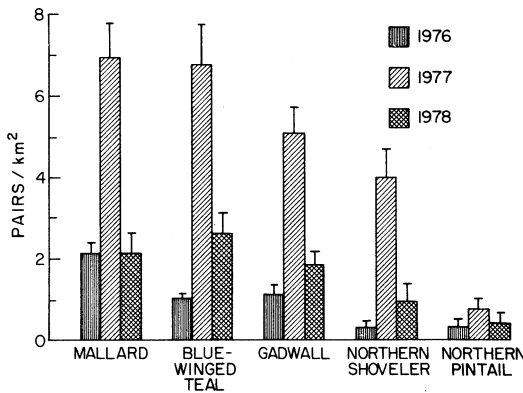


Fig. 1. Relative densities (\bar{x} and upper 95% CL) of dabbling duck indicated pairs (pairs plus lone males) extrapolated from observed mean densities in random 16.2-ha subunits throughout east Delta Marsh, Manitoba, 1976–78.

to the survey (e.g., human activity, ice cover, marsh fires). Hence, yearly sample sizes are less than the product of numbers of surveys times random subunits.

RESULTS

Yearly Pair Densities and Water Level Conditions

Over all surveys and years, mallard and blue-winged teal were most abundant, followed by gadwall, northern shoveler, and northern pintail (Fig. 1). Pair densities varied among years. The most dramatic change occurred in 1977, when mean densities of all species except northern pintail rose sharply (≥ 3 times). Blue-winged teal, gadwall, and northern shoveler densities were greater ($P < 0.05$) in 1978 than 1976.

Yearly changes in pair densities accompanied water level fluctuations (Fig. 2). Although water levels for April 1976 were not available for comparison, mean levels for May and June 1976 were considerably greater than levels during April–June 1977 and 1978. Average levels for May and June 1976 approached full-supply level (i.e., 248 m above sea level; Geodetic Survey of

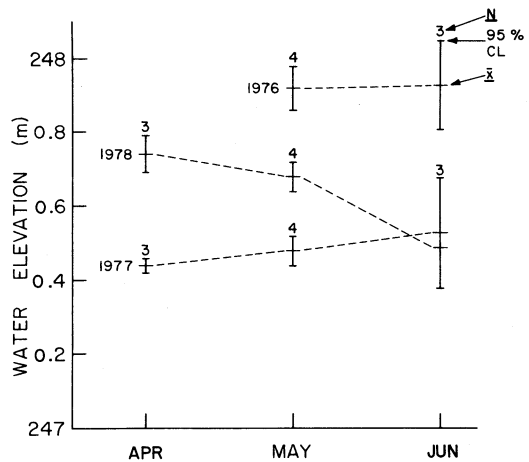


Fig. 2. Relative water levels (above sea level) in east Delta Marsh, April–June 1976–78. Levels for May 1976 obtained from Sioux Pass gauge; all others obtained from Cadham Bay gauge. Confidence interval for June 1978 mean level is not shown; it completely overlaps 1976 and 1977 intervals.

Canada) for the east Delta Marsh. Water levels declined during summer and autumn 1976, resulting in a recorded spring-time low of 247.43 m on 27 April 1977. A slight increase ensued during May and June 1977. Spring 1978 mean water levels were intermediate among the 3 years and had a seasonal downward trend.

Breeding Pair–Habitat Associations

To demonstrate patterns in dabbling habitat use across species and years, we performed separate regressions for each of the five species and 3 years. The 15 regressions of dabbling pair densities against the explanatory variables varied in levels of significance ($0.001 \leq P \leq 0.014$) and multiple correlation ($0.22 \leq R \leq 0.60$). The signs of standardized regression coefficients for retained variables matched those of corresponding simple correlation coefficients for each dependent–explanatory variable relationship. Flake et al. (1977) and Roberson (1977) caution that intercorrelated explanatory variables can lead to incongruent signs on the afore-

Table 1. Variables relating to dabbling duck pair numbers in 16.2-ha sample areas of the east Delta Marsh, Manitoba, 1976–78, as revealed by stepwise multiple regression.

| Species | Variable ^a | Original standardized regression and multiple correlation coefficients ($\times 100$) | | |
|-------------------|--|---|---------------------------|--------------------------|
| | | 1976 (<i>N</i> = 229) | 1977 (<i>N</i> = 221) | 1978 (<i>N</i> = 52) |
| Mallard | Forest (<i>FOR</i>) | | -173 | |
| | Vegetation–water interspersions (<i>VWI</i>) | 4 | 16 | 4 |
| | Emergent-habitat richness (<i>EHR</i>) | 4 | | |
| | Whitetop–sedge (<i>WS</i>) | 33 | | |
| | Cattail–bulrush (<i>CB</i>) | | 30 | 36 |
| | Survey number (<i>SN</i>) | | -10 | |
| | | <i>R</i> ^b = 44 | 60 | 49 |
| Blue-winged teal | Forest | | -183 | |
| | Vegetation–water interspersions | | 14 | |
| | Emergent-habitat richness | 4 | | |
| | Common reed (<i>CR</i>) | | 53 | 74 |
| | Whitetop–sedge | 31 | | |
| | Cattail–bulrush | | 54 | 57 |
| | | 2 | | 8 |
| | | <i>R</i> = 36 | 51 | 60 |
| Northern shoveler | Forest | 61 | -162 | |
| | Vegetation–water interspersions | | 6 | |
| | Emergent-habitat richness | | | 10 |
| | Shoreline development (<i>SD</i>) | | 116 | |
| | Common reed | 20 | | |
| | Whitetop–sedge | 26 | | |
| | | | 36 | |
| | | <i>R</i> = 33 | 40 | 42 |
| Gadwall | Forest | | -239 | |
| | Vegetation–water interspersions | | 8 | |
| | Emergent-habitat richness | 5 | 10 | |
| | Shoreline development | | | 12 |
| | Whitetop–sedge | | -36 | |
| | Cattail–bulrush | | | 38 |
| | | 2 | -5 | |
| | | <i>R</i> = 24 | 48 | 42 |
| Northern pintail | Forest | | -37 | |
| | Vegetation–water interspersions | 1 | 2 | 3 |
| | Shoreline development | 3 | | |
| | Whitetop–sedge | 9 | | |
| | | <i>R</i> = 22 | 22 | 34 |

^a Defined in Methods. Variables' abbreviations in parentheses; each abbreviation given once in table.

^b Multiple correlation between species' pair densities and variables retained ($P \leq 0.1$) by stepwise process.

mentioned coefficients and potential misinterpretation of dependent–independent variable relationships.

Explanatory habitat variables varied in frequency of association with dabbling pair densities, direction (i.e., + or -) and extent of influence, and yearly occurrence

as habitat correlates. Most habitat variables exhibited positive associations with dabbling pair densities (Table 1). Both indices, vegetation–water interspersions (*VWI*) and shoreline development (*SD*), quantify relative amounts of emergent vegetation–water interspersions. *VWI* and

SD together were correlated with dabbling pair densities 12 times in 15 regressions. Although *VWI* exhibited less influence on dabbling pair densities in comparison to other habitat correlates, it was the most frequent habitat correlate, being retained in 9 of 15 regressions. Mallard and northern pintail pair densities were associated with *VWI* in all 3 years, whereas variation in blue-winged teal, northern shoveler, and gadwall pair densities was linked with *VWI* only in 1977. The relative influence of *VWI* on yearly variation in mallard pair densities was greater in 1977 than in either 1976 or 1978. Its influence on northern pintail densities was similar among years. Additionally, northern pintail, northern shoveler, and gadwall pair densities were related to *SD* in 1976, 1977, and 1978, respectively.

The positive correlation between dabbling pair densities and emergent habitat richness (*EHR*) seemed linked to the occurrence of associations between certain species pair densities and *VWI*. *EHR* and *VWI* were moderately correlated in 1976 ($r = 0.51$, $N = 229$), 1977 ($r = 0.49$, $N = 221$), and 1978 ($r = 0.65$, $N = 52$), suggesting that the variables competed for entry into the regression models. *EHR* was retained, but *VWI* was not, in three models (i.e., blue-winged teal and gadwall in 1976, northern shoveler in 1978) (Table 1). In two additional models, both *EHR* and *VWI* occurred, each exerting a similar amount of influence on species pair densities (i.e., mallard in 1976, gadwall in 1977).

All five dabbling species showed an association with the proportional cover of whitetop rivergrass-sedge (*WS*) (Table 1). Mallard, blue-winged teal, northern shoveler, and northern pintail pair densities were positively associated with *WS* in 1976; gadwall pair densities were negatively associated with *WS* in 1977. Ex-

amination of regression coefficients for variables retained by the analysis of 1976 data suggested that *WS* exerted a major influence on dabbling pair densities.

With the exception of northern pintail, the proportional cover of cattail-bulrush (*CB*) was relatively strongly associated with dabbling pair densities in 1977 and/or 1978 (Table 1).

Variation in dabbling pair densities was least frequently correlated with the proportional cover of common reed (*CR*). Positive associations between pair densities and *CR* arose for blue-winged teal in 1977 and 1978 and northern shoveler in 1976 (Table 1).

The proportional cover of forest (*FOR*) was the only habitat variable consistently negatively associated with dabbling pair densities. A negative association emerged for all five species in 1977 (Table 1); only northern shoveler pair densities in 1976 were positively related to *FOR*. When retained by the stepwise process, *FOR* was the dominant habitat correlate of dabbling pair density.

Dabbling Duck Species Richness

Separate yearly regressions revealed that variation in dabbling duck species richness was significantly ($P \leq 0.001$) associated ($0.55 \leq R \leq 0.76$) with the retained explanatory variables. The pattern of habitat associations with dabbling species richness resembled that of species pair densities (Table 2). Species richness and *VWI* were positively associated in all 3 years, with *VWI* displaying its greatest relative effect in 1977. Correlation between *VWI* and *EHR* may have similarly affected their association with species richness; both variables exerted similar positive influences on dabbling species richness in 1976 and 1977. A positive association between dabbling species richness and *WS* was only

Table 2. Variables relating to the number of dabbling duck species in 16.2-ha sample areas of the east Delta Marsh, Manitoba, 1976–78, as revealed by stepwise multiple regression.

| Variable ^a | Original standardized regression and multiple correlation coefficients (×100) | | |
|--|---|-------------------|------------------|
| | 1976 (N = 229) | 1977 (N = 221) | 1978 (N = 52) |
| Forest (<i>FOR</i>) | | –257 | |
| Vegetation–water interspersions (<i>VWI</i>) | 5 | 13 | 6 |
| Emergent-habitat richness (<i>EHR</i>) | 6 | 14 | |
| Common reed (<i>CR</i>) | 29 | | 97 |
| Whitewort–sedge (<i>WS</i>) | 63 | | |
| Cattail–bulrush (<i>CB</i>) | | 41 | 92 |
| Survey number (<i>SN</i>) | | –3 | |
| | <i>R</i> ^b = 55 | 70 | 76 |

^a Defined in Methods. Variables' abbreviations in parentheses.

^b Multiple correlation between number of dabbling species and variables retained ($P \leq 0.1$) by stepwise process.

evident in 1976, when *WS* exhibited the highest relative influence of all variables on species richness. In 1977 and 1978, dabbling species richness was positively associated with *CB* and in 1976 and 1978 with *CR*. The only negative correlate of species richness was *FOR* in 1977.

Intraseasonal Variation in Pair Densities and Species Richness

Although we suspected a nonlinear trend in intraseasonal variation of species pair densities and richness, the high deviation in plots of the dependent variables against survey number (*SN*) obscured any potentially existing nonlinear trend. Because the plots did not depict any clear nonlinear pattern, we included *SN* linearly in the multiple regression analyses.

Variation in blue-winged teal pair densities in 1976 and 1978 and in gadwall pair density in 1976 was weakly positively associated with *SN* (Table 1). Both are relatively late nesting species, possibly explaining their numeric increase as seasons progressed. We found an inverse association of mallard and gadwall pair densities and dabbling duck species richness with *SN* in 1977 (Tables 1, 2).

DISCUSSION

Drought Responses

Pair densities of all species except northern pintail increased significantly in 1977. Coincident with the increases was severe drought throughout the northern plains. We believe the increases were largely due to influxes of birds displaced from drought-stricken habitats. Several studies (e.g., Trauger and Stouder 1978, Jackson 1979, Derksen and Eldridge 1980, Giroux 1981, Mulhern 1982) documented a similar trend for 1977. The Delta Marsh appears not only to support breeding, juvenile, molting, and migrant waterfowl, but also apparently offers important residual habitat for dabbling ducks and presumably other species of drought-displaced marsh birds.

If there had been a major influx of northern pintail into the Delta Marsh from other areas in 1977, our surveys should have detected it. Drought-displaced northern pintail may have migrated to more northern latitudes (Smith 1970, Henny 1973, Derksen and Eldridge 1980) rather than to permanent prairie marshes like Delta. However, we may have been unable to detect a significant difference in

northern pintail density partly because the species is locally sparse; hence any difference in absolute numbers of northern pintail in 1977 would not be nearly as great as for the more abundant species.

Despite the sharp increases, pair densities of the five species were $\frac{1}{27}$ – $\frac{1}{2}$ as high as densities recorded by Kaminski and Prince (1981*b*) in 1977 during ground surveys of an experimentally manipulated, flooded shallow-marsh habitat in the east Delta Marsh. We suspect that helicopter surveys were less effective than ground surveys for censusing, but also speculate that habitat conditions in the experimental area (e.g., flooded shallow marsh with numerous open water areas) promoted high dabbling use.

Habitat Correlates

Several consistent patterns of habitat correlation emerged across species and years for dabbling pair densities and across years for dabbling species richness. These were (1) a dominant, negative association of all species pair densities and richness with *FOR* in 1977; (2) a positive association of species pair densities and richness with *WS* in 1976; and (3) a frequent association of species pair densities and richness with *VWI*. We will endeavor to explain these patterns.

FOR and WS.—A somewhat perplexing pattern was the strong negative association of dabbling pair densities and species richness with *FOR* for 1977 data. Intuitively, we predicted such a relationship for all years. Why did this relationship emerge only for 1977? The association appears to be an artifact of the extremely low water levels in the Delta Marsh during 1977. Forested habitat is almost exclusively restricted to the narrow beach ridge separating Delta Marsh from Lake Manitoba. Contiguous with the forested ridge is a shallow-marsh zone (com-

mon plants include awned sedge, white-top rivergrass, and cattail [Stewart and Kantrud 1971]) that is flooded to variable depths in spring, depending on water levels of the marsh and adjoining Lake Manitoba and runoff from snow accumulations along the beach ridge. Water-level data indicated that 1977 spring levels were well below 1976 and 1978 levels. Based on topographical elevations in the vicinity of the ridge and observations of flooding conditions, we propose that 1977 water levels were insufficient to inundate the forest-contiguous wetland zone. The shallow or complete absence of flooding probably limited dabbling access to this zone, causing *FOR* to elicit the observed negative influence. Additional evidence supporting this explanation is (1) the contrasting positive association between northern shoveler pair densities and *FOR* in the high-water year of 1976; (2) the negative relationship between gadwall pair densities and *WS* during 1977, and, most importantly; (3) the positive associations of four of five species pair densities and species richness with *WS* in 1976, when dabbling use of the shallow-marsh zone was apparently not constrained by inadequate flooding. Similarly, Bishop et al. (1979) and Weller (1979) related variation in numbers of indicated breeding blue-winged teal to fluctuations in water level and extent of flooding within shallow-marsh zones of several Iowa marshes. In the prairie pothole region of North Dakota, Kantrud and Stewart (1977) reported high densities of indicated breeding dabblers in temporary and seasonal wetlands when flooded. The latter wetlands are ecologically similar to the seasonally flooded shallow-marsh zone of prairie glacial marshes.

When *WS* occurred as a habitat correlate concomitant with high water, its comparatively high regression coefficients are perhaps indicative of the importance of

flooded shallow-marsh habitats to breeding dabblers. Previous workers have reported associations between breeding dabblers and different resources characteristic of shallow-marsh zones, including rich invertebrate fauna (Swanson et al. 1974), potential territorial space (Weller 1979, Kaminski and Prince 1981*b*), nesting cover (Sowls 1955, Krapu et al. 1979), and loafing-roosting sites (Drewien and Springer 1969, Weller 1979).

VWI.—Although *VWI* was not the strongest positive habitat correlate, its frequent individual occurrence coupled with that of *SD* suggests that emergent vegetation–water interspersions does influence dabbler pair densities and species richness. However, its importance seemingly varies relative to yearly water-level conditions. The regression analyses revealed a positive association of only mallard and northern pintail pair densities and species richness with *VWI* in all 3 years. In contrast, blue-winged teal, northern shoveler, and gadwall pair densities were related to *VWI* only in 1977 and northern shoveler and gadwall densities with *SD* in 1977 and 1978, respectively. Perhaps the latter associations reflect dabblers' avoidance of, or inability to occupy, the shallow-marsh zone in low-water years. Depressed water levels in 1977 and 1978, resulting in inadequate or no flooding within the shallow-marsh zone, may have forced dabblers to occupy slightly lower marsh elevations where generally permanent open water is interspersed with robust emergents (e.g., cattail and tule bulrush). Further evidence for this explanation is the positive association of mallard, blue-winged teal, northern shoveler, and gadwall pair densities and dabbler species richness with *CB* in 1977 and/or 1978. However, our method of quantifying *VWI* and *SD* from summer aerial imagery tends to emphasize interspersions between gen-

erally permanent open water and robust emergents. The method does not accurately estimate *VWI* that would be present in shallow-marsh habitats during a wet spring. Thus, *VWI* might have showed increased frequency of association and importance had we been able to quantify its occurrence within the shallow-marsh zone during spring 1976.

The markedly lower water levels in 1977 may have allowed dabbler exploitation of the abundant invertebrate resource (predominantly Chironomidae larvae) in the otherwise deeper bays of the Delta Marsh (Kaminski and Prince 1981*a*). For 1977, Kaminski and Prince (1981*a*) reported that all five dabbler species foraged more frequently in response to higher invertebrate resources in two open bays fringed by cattail and tule bulrush than in an adjacent manipulated and artificially flooded shallow-marsh habitat of the Delta Marsh.

We can only speculate why only mallard and northern pintail showed a positive association with both *WS* and *VWI* in 1976. Both species are highly mobile in comparison to other dabbler species and consequently exhibit larger breeding home ranges (Nudds and Ankney 1982). This trait may have resulted in both species' home ranges extending over or including more habitat types, thus increasing the likelihood for associations with *WS* and *VWI*.

Within flooded emergent habitats, the degree of *VWI* may influence levels of occupancy by dabbling duck pairs. *VWI* and cover of open water are related; a predominance of the latter typically results in decreased *VWI* and consequently reduced numbers of dabbling duck pairs and species. In Delta and probably other marshes, abundant *VWI* (a result of *SD*, lodged and flooded-over emergents, and occurrence of intramarsh potholes and

creeks) may enhance the availability of surface isolation from conspecific pairs and thereby increase pair occupancy per unit area. We propose that *VWI* influences occupancy potential and use of flooded emergent habitats by dabbling ducks as do wetland numbers in pothole environments (e.g., Stewart and Kantrud 1974, Bellrose 1979). In an earlier paper (Kaminski and Prince 1981*b*), we also suggested that dabblers may use *VWI* as a proximate cue to habitats rich in aquatic invertebrates. Moreover, we report here that with increased cover of open water, decreased *VWI* and habitat structural diversity (i.e., *EHR* and plant community edge) ensue. Therefore, breeding dabbler abundance and species richness within flooded emergent habitat may relate to the effects that *VWI* manifests upon isolated pair space, aquatic invertebrate resources, and habitat structural diversity.

We predicted a positive linear relationship of dabbler pair densities and species richness with *VWI*. Examination of plots of species pair densities and richness against *VWI* did not reveal any obvious nonlinear patterns, although nonlinearity could have been obscured by the variance in the data. Previous investigations have shown that, along a gradient of increasing cover of open water, decreased marsh bird abundance and diversity occur with increasing departures from a 1:1 vegetation-water ratio. For example, Weller and Spatcher (1965) and Weller and Fredrickson (1973) reported that avian abundance and diversity in several Iowa marshes were highest during periods of marsh succession when emergent vegetation and open water covered approximately equal areas in a highly interspersed pattern. Kaminski and Prince (1981*b*) and Murkin et al. (1982) presented experimental evidence corroborating this phenomenon by showing the occurrence of highest dabbler pair

densities and species diversity in plots artificially manipulated to provide a 1:1 ratio of open water and emergent vegetation.

Results of the regression analyses led us to hypothesize that flooding of the shallow-marsh zone and *VWI* within emergent habitats are important habitat influences of dabbling duck pair densities and species richness in the Delta Marsh and possibly other marshes. The seemingly dominant influence of flooded shallow-marsh habitat over *VWI* may indeed be real in view of the variety and abundance of resources potentially available in this habitat type. In wet years, dabblers and other marsh birds respond to resources (e.g., aquatic foods, over-water nest sites, isolated pair space, etc.) within the shallow-marsh zone that become available only under flooded conditions. In addition, we feel that the interspersion of open water throughout this often densely vegetated zone is important because it allows ducks access to these resources.

MANAGEMENT IMPLICATIONS

The multiple regression analyses revealed several interpretable patterns of habitat correlations. However, as recently emphasized by Wiens and Rotenberry (1981*a*:531), "... correlation does not necessarily imply that the relationships are directly causal and meaningful to the birds; ... to proceed to frame management policies upon them would be premature." We are cognizant of these potential dangers and therefore proceed cautiously in offering considerations for habitat management in large marshes.

The positive associations of dabbler pair densities and species richness with *WS* in the high-water year, coupled with the negative effect imposed by *FOR* in the low-water years, suggest that regulated spring flooding of the shallow-marsh zone

may be a beneficial management practice for breeding ducks. Inundation of this zone would enhance dabbler and diver access to the protein- and calcium-rich invertebrate foods necessary for egg production (Krapu 1979:68), as well as other resources identified earlier. Over-water nesting species would also benefit, considering R. D. Sayler's (unpubl. rep., Inst. Ecol. Stud., Univ. North Dakota, Grand Forks, 1983) findings of increased canvasback (*Aythya valisineria*) and redhead (*A. americana*) nest densities and success in a year when the shallow emergent habitats of the Delta Marsh were well flooded. However, if temporary spring "back flooding" is contemplated to improve shallow-marsh habitat for waterfowl and forage production, suitable brood-rearing habitat must be available nearby so as not to strand flightless young upon summer drawdown (MacLennan 1977). High benefit-cost ratios would predictably result if researchers formulated recommendations based on field experiments that addressed both wildlife and agricultural interests. A more comprehensive investigation such as this was undertaken by H. Neckles (unpubl. rep., Delta Waterfowl Res. Stn., Delta, Manit., 1982), who experimentally examined waterfowl use, invertebrate resources, and yields of whitetop rivergrass in the Delta Marsh in response to several flooding regimes.

The present study and several others (e.g., Weller and Spatcher 1965, Weller and Fredrickson 1973, Bishop et al. 1979, Kaminski and Prince 1981b, Murkin et al. 1982) empirically support our suggestion that abundant vegetation-water interspersions are an important positive correlate of spring dabbling duck use of prairie marshes. Enhancing vegetation-water interspersions is frequently achieved through water-level manipulation. Raising water levels stimulates natural opening of dense-

ly overgrown marshes. In predominantly open-water marshes, reestablishment of emergent vegetation can occur in response to natural drought or artificial drawdown that exposes the marsh bottom and promotes germination of accumulated seeds (van der Valk and Davis 1978:322). Prairie glacial marshes typically harbor rich seed banks, thus underscoring the potential for use of water-level management to stimulate revegetation and production of waterfowl foods. We recommend artificial drawdown (complete or partial) as a technique to encourage revegetation, inasmuch as it simulates natural drought as well as often being an economical and expedient treatment for large basins. Time of drawdown (i.e., spring or fall) at northern latitudes will partly depend on whether overwinter survival of muskrats (*Ondatra zibethicus*) is important. Before implementing water-level management, biologists must ascertain the adequacy, composition, and distribution of the seed bank to ensure the desired (or expected) response. This was emphasized by Pederson (1981), who showed that emergent seedling densities (e.g., *Scirpus validus*, *Typha* spp.) in substrate samples from large open bays of the Delta Marsh are low in comparison to samples extracted from shoreline emergent habitats. Therefore, complete dewatering of large open bays with the objective of revegetation could produce disappointing results. Pederson (1981) proposed several options designed to exploit (i.e., through irrigation techniques or partial drawdowns) the large seed banks of the shoreline emergent zone. Kadlec (1982) and Lieffers and Shay (1983) described procedures (i.e., irrigation, dilution, drying, and reflooding) for reducing sediment and water salinity to promote establishment of emergent macrophytes.

Multiple regression or correlation anal-

yses are useful procedures for coupling bird species abundances (or other parameters) with measured habitat variables (Wiens and Rotenberry 1981a:530). In addition, the techniques are valuable for gaining insight into potential bird-habitat relationships from which hypotheses can be formulated and, ultimately, experiments conducted to test hypotheses. Multiple regression can also be used to quantitatively predict values of dependent variables from measured explanatory variables. In this study, variation in dabbling species pair densities and richness was not strongly linked with measured habitat variables, as evidenced by the relatively low *R* values. We suggest that habitat variables alone cannot be expected to produce precise predictions of dabbling duck pair densities or species richness in a general approach such as ours. However, habitat variables might serve admirably as ancillary variables to increase precision of population estimates from large-scale survey efforts (Johnson 1981). In future similar investigations, perhaps measurement of more (preferably truly independent) variables would improve precision. For example, we recommend adding average ground elevation of survey marsh units as an explanatory variable if an accurate contour map is available. Knowledge of elevation along with water-level records from permanent gauges would reveal the relative extent and depth of flooding within different emergent zones and potentially aid in interpreting patterns of waterfowl habitat use. If a multivariable approach is contemplated and intercorrelation exists among the habitat variables, researchers might profit by exploring the combined application of principal component analysis and multiple regression analysis (Green 1979:117).

Habitat correlational investigations are useful for exposing patterns of species or

community attributes and the environment. Developing interpretable relationships from such studies can be an important first step toward design and conduct of future hypothetico-deductive research (Romesburg 1981). The present study implicates use of water-level management to improve northern prairie marshes primarily for breeding dabbling ducks. Subsequent research should focus on use of marshes by other avian guilds during and outside the breeding season. Moreover, researchers and resource managers should develop and publish water-level management practices for major wetland systems (Cowardin et al. 1979) designed to yield wildlife and societal benefits.

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