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Author(s): Richard M. Kaminski and Harold H. Prince

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DABBLING DUCK AND AQUATIC MACROINVERTEBRATE RESPONSES TO MANIPULATED WETLAND HABITAT¹

RICHARD M. KAMINSKI,² Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824
HAROLD H. PRINCE, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824

Abstract: Responses of breeding dabbling ducks (Anatini) and aquatic macroinvertebrates to experimental modifications of cover:water ratio and basin surface were investigated in 1977 and 1978 within an impounded whitetop rivergrass (*Scolochloa festucacea*) meadow on the Delta Marsh, south-central Manitoba. Three areal percentage ratios of emergent hydrophytes to open water (30:70, 50:50, or 70:30) and 2 basin treatments (mowing of existing emergents or scarification by rototilling) were tested. Between years, pair numbers of mallards (*Anas platyrhynchos*) and blue-winged teal (*A. discors*) declined, whereas pair numbers of northern shovelers (*A. clypeata*), gadwalls (*A. strepera*), and pintails (*A. acuta*) were comparable. The greatest density and species diversity of dabbling duck pairs occurred on 50:50 plots in both years. Only blue-winged teal and pintail pair densities in 1978 were greater on mowed than on rototilled areas. Within years, species diversity of dabbling ducks was unaffected by mowing or rototilling. More pursuit flights arose from 50:50 plots and mowed areas compared to alternative treatments. Composition and resource levels (abundance, biomass, and number of families) of aquatic macroinvertebrate communities varied within and between years in response to basin treatments. These results imply prescriptions for wetland habitat management.

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The interaction of proximate and ultimate factors continues to intrigue ecologists studying avian habitat selection. Since the pioneering work by Beecher (1942) and Svårdson (1949), significant theoretical advances in our understanding of the evolution of habitat selection have emerged (e.g., MacArthur and Levins 1964, Fretwell and Lucas 1969, Bryant 1973, Rosenzweig 1974, Southwood 1977). Generally, theory predicts that animals should select habitats that maximize fitness. Unfortunately, the complexity of such a prediction makes hypothesis testing impractical under most environmental conditions.

Habitat selection in birds is seemingly guided by instinctive and experiential influences from the physical and/or social environment (Hildén 1965). Numerous

attempts have been made to identify key factors associated with habitat selection within and among bird species. Most investigators have correlated bird species abundance or diversity with environmental variables, and therefore cannot distinguish between habitat selection and habitat correlation (Wiens 1976). True habitat selection occurs when individuals exercise a choice among available habitats, instead of differentially occupying them as a consequence of extrinsic factors like predation and competition (Klopfer 1969; Wiens 1976, 1977). In field investigations, however, it is not usually possible to control extrinsic factors.

Only rarely have researchers studied avian habitat selection using experimental procedures (e.g., Klopfer 1963, Partridge 1974). The experiment described here was designed to investigate the effects of habitat structure and resource levels of aquatic macroinvertebrates on habitat use by breeding dabbling ducks. Most literature on this subject originates from studies conducted in prairie-pot-

¹ Contribution 9125, Michigan State University Agricultural Experiment Station.

² Present address: Ducks Unlimited (Canada), 1190 Waverley Street, Winnipeg, Manitoba R3T 2E2, Canada.

hole habitats of the United States and Canada. Consequently, our understanding of habitat use by breeding dabbling ducks on large marshes is inadequate. Weller and Spatcher (1965) and Weller and Fredrickson (1974), studying several marshes in Iowa, reported that avian abundance and diversity were highest during years when emergent hydrophytes and open water covered approximately equal areas in a highly interspersed pattern. They termed this stage of marsh transition the hemi-marsh phase. Inspired by their work, we conducted an experiment on the Delta Marsh, south-central Manitoba, to test the hypothesis that there would be unequal responses in density and species diversity of breeding dabbling ducks to differing combinations of emergent vegetation and open water, and to modifications of basin surface. Moreover, we tested the hypothesis that differences in abundance, biomass, and familial diversity of aquatic macroinvertebrates would result in response to these treatments.

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STUDY AREA

The study was conducted on a 33-ha tract of the Delta Marsh in south-central Manitoba (50°11'N, 98°19'W), approximately 2 km east of the Delta Waterfowl Research Station. A detailed description of the local physiography was provided by Fenton (1970), and the floristic communities have been thoroughly described (Hochbaum 1944, Love and Love 1954, Olsen 1959, Walker 1965, Anderson and Jones 1976).

A wooded beach ridge separating Lake Manitoba from the Delta Marsh formed the northern boundary of the study area. In March 1977, an earthen dike was constructed around the southern reach of the area so water levels could be controlled. Originally, an unbroken dense stand of emergent hydrophytes covered the area. Thus, there was no existing natural interspersed vegetation and open water to confound experimental levels of interspersed vegetation. The predominant plant species was whitetop rivergrass; it covered 60% of the study area. Other emergents included giant reed (*Phragmites australis*) (30%), common cattail (*Typha latifolia*) (5%), and sedges (*Carex* spp.) (5%). The soil was a histisol (Buckman and Brady 1969:319).

METHODS

Habitat Manipulations

In July 1976, 18 square plots (1 ha) were established by permanently marking their corners with 5.5-m wooden poles. Plots were irregularly placed in close juxtaposition to permit inclusion of all plots within the impoundment. Habitat manipulations began in August 1976 when the soil was sufficiently dry to support a tractor and rotary mower.

A diagrammatic example of plot design

is shown in Fig. 1. Each plot provided 1 of 3 areal percentage ratios of emergent vegetation to open water (30:70, 50:50, or 70:30) and 1 of 2 basin treatments (mowing of existing vegetation or scarification by rototilling). This furnished 3 replicates of 6 treatment combinations, which were randomly assigned to plots. Vegetation was mowed with a tractor-drawn rotary mower within 3, 5, or 7 0.1-ha circles to create open-water areas (upon inundation) of 30, 50, or 70%, respectively, per 1-ha plot (Fig. 1). The centers of circles were randomly located from 9 possible points per plot to minimize positional bias. Plant litter from mowing was left lying. Before rototilling designated circles in 1976, it was necessary to remove the litter. This was accomplished by consolidating litter into piles with a side-delivery hay rake and then burning them. Burning prior to the second rototilling operation in 1977 was not necessary due to reduced plant regeneration. Concentric paths were followed while mowing and rototilling to distribute treatment effects evenly. Plot treatments of 1976 were repeated in August 1977 in preparation for the 1978 season.

The impoundment was inundated between 11 and 19 April in 1977 and 1978 by pumping water from the Delta Marsh. This was approximately 2 weeks before peak numbers of dabbling duck pairs arrived on the study area each year. Water was present in all circles following inundation, and analysis of variance (ANOVA) revealed no differences ($P > 0.05$) in weekly samplings of water depths among 5 sites randomly located within the impoundment. Water depth was maintained at 32 ± 3 cm until 3–7 June in 1977 and 1978, when water levels were completely drawn down. The study was terminated on 30 May in both years because growing vegetation biased inter-

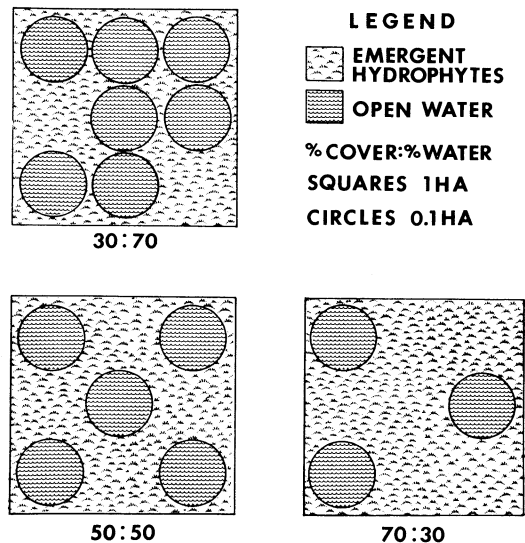


Fig. 1. Diagrammatic examples of experimental plots.

spersion levels and complicated observations of ducks.

Breeding Pair Surveys

Six morning helicopter (Bell 47G-4A) surveys were conducted biweekly in 1976 (12 April–21 June) to estimate pre-treatment numbers of indicated pairs (pairs and single males) of dabbling ducks on the study area and other areas of the Delta Marsh. In 1977 and 1978, indicated-pair use of the study area was estimated through ground counts made 3 times weekly (0730 Tuesday, 1500 Thursday, 1830 Sunday) between 19 April and 28 May. Usually 1.5 hours were required to complete a ground survey. During ground surveys, an observer walked through the 18 plots and relayed information (plot number, dabbler species, pair or single male) via radio to an assistant, in an elevated blind, who visually followed (using binoculars when necessary) the flight route of flushed birds. To prevent duplicating pair counts, the observer was informed of previously

counted birds that alighted on plots yet to be surveyed.

Ground-count data were used to compute Brillouin's index of species diversity (H). The index, taken from information theory, combines species richness and equitability of abundance among species. It is appropriate when individuals of a finite number of populations are identified and enumerated from nonrandomly selected sample areas (Poole 1974:388), a situation applicable to our study. The general equation is

$$H = \frac{1}{N} \log_e \frac{N!}{N_1! N_2! N_3! \dots N_s!},$$

where N = total number of indicated pairs of all species, and N_i = number of indicated pairs of species i , $i = 1, 2, 3, \dots, s$.

While observing activities of unmarked dabbling ducks in 1978, pursuit flights (i.e., aerial chase of an intruding pair by a territorial male conspecific) originating from treatment plots were recorded. The plot of origin was determined by observing either the initiation of a flight or the return location of a defending male. To prevent duplication, 2 observers compared notes on flight initiation times, directions, and subsequent return locations.

Aquatic Macroinvertebrates

Samples of aquatic macroinvertebrates were collected weekly throughout the 1977 and 1978 study seasons. One sample was collected from the approximate center of each of 10 mowed and 10 rototilled 0.1-ha circles selected randomly and contained within plots representing each cover-water treatment. Ten randomly located open-water sites within a bay of the Delta Marsh adjacent to the impoundment were also sampled; the untreated bay was designated as the control

area. Depth of water at each site was measured. A single-core sampler (50-cm plastic pipe, 8.5-cm in diameter), illustrated by Merritt and Cummins (1978:22, Fig. 3.11), was used to sample rototilled circles and control sites. The corer did not function on mowed circles because of interference by plant litter. Instead a device, modified after Gerking (1957), consisting of a steel-rod frame (21 × 52 × 107 cm) covered with nylon netting (0.5-mm apertures), was used to sample mowed plots. Immediately following collection, samples were returned to the lab for analysis. Samples taken with the corer were combined with a liberal volume of sucrose solution (1 kg sugar/2 liters water), which floated invertebrates to the surface for ease of sorting (Flannagan 1973). Invertebrates were identified to family, using Pennak (1953) and Merritt and Cummins (1978), and counted. A sample from each family was oven-dried (105 C) for 24 hours (Cummins and Wuycheck 1971) and then weighed on a Mettler H-54 balance.

Analytic Procedures

Statistical analyses, following Sokal and Rohlf (1969), Nie et al. (1970), or Gill (1978), included parametric and nonparametric tests. Assumptions of ANOVA were met by transforming data by either square root or log procedures (Gill 1978:159). Variation around means is expressed as either 1 standard error or 95% confidence intervals for back-transformed estimates.

RESULTS

Temporal Variation

Although the study area was inundated naturally during the pretreatment season of 1976, few indicated pairs (hereinafter called pairs) of dabbling ducks were ob-

served from the helicopter. An average of 2 pairs per survey ($N = 6$) was observed in 1976, contrasted with averages of 73 ($N = 18$) and 43 ($N = 15$) pairs for treatment-period ground surveys in 1977 and 1978, respectively.

Seven species of dabbling ducks were observed using the impoundment in 1977 and 1978. American wigeon (*A. americana*) were present in low numbers and green-winged teal (*A. crecca*) occurred as transients; thus, analyses were limited to mallards, blue-winged teal, northern shovelers, gadwalls, and pintails.

Early-returning (4–14 April, 1977 and 1978) mallards and pintails initially used portions of the study area where “sheet” water accumulated. Inundation of the area was delayed until 11–19 April in both years because ice conditions on the Delta Marsh prevented earlier flooding. As flooding progressed, pairs and groups of dabbling ducks moved onto the unit. Approximately equal numbers of pairs were observed during the 1st week each year. Mean pair numbers for all dabbling species per ground survey peaked at 97 ± 3 (SE, $N = 3$) and 53 ± 10 (SE, $N = 3$) during 1–7 May in 1977 and 1978, respectively. By late May, mean pair numbers declined to approximately 40% of peak numbers. Differences between years in mean numbers of pairs during May were attributed to marked changes in pair numbers of mallards and blue-winged teal (Table 1). Mallard and blue-winged teal mean pair numbers decreased by 68 and 44%, respectively, between 1977 and 1978, whereas shoveler, gadwall, and pintail pair numbers were comparable.

Weather

Weather records were obtained from the University of Manitoba Field Station

Table 1. Pairs of dabbling ducks observed during ground surveys conducted between 19 April and 28 May in 1977 and 1978.

Species	1977 (18) ^a		1978 (15)	
	\bar{x}	SE	\bar{x}	SE
Mallard	28 ^b	2	9 ^c	1
Blue-winged teal	34 ^b	4	19 ^c	3
Shoveler	7 ^b	1	6 ^b	1
Gadwall	3 ^b	1	5 ^b	1
Pintail	2 ^b	1	3 ^b	1
Grand mean	73 ^b	5	43 ^c	4

^a Number of ground surveys.

^{b,c} Row means with unlike superscripts are different ($P < 0.05$) by Mann-Whitney U test.

located approximately 6 km west of the study area. Stepwise multiple regression was used to examine the relationships among 5 meteorologic variables (ambient temperature, pyrheliometer index, wind speed and direction, presence or absence of rain) and the total number of pairs of a dabbling species per ground survey. None of the variables was related ($P > 0.05$) to species pair numbers in 1977 ($N = 18$) or 1978 ($N = 15$), suggesting that variation in dabbling pair numbers on the study area was not influenced by local weather changes.

Pair Densities

The effects of habitat treatments (vegetation-to-water percentage ratios and basin treatments) and survey time (morning, afternoon, or evening) on weekly variation in mallard and blue-winged teal pair densities were analyzed using a 3-factorial ANOVA. These species were abundant both years; few (<10%) replicates per treatment combination had zero values. Designed comparisons among means of significant main effects were made with Bonferroni t statistics, a procedure appropriate for nonorthogonal contrasts (Gill 1978:176). Shoveler, gadwall, and pintail pairs were not as numerous (37–75% of the replicates had

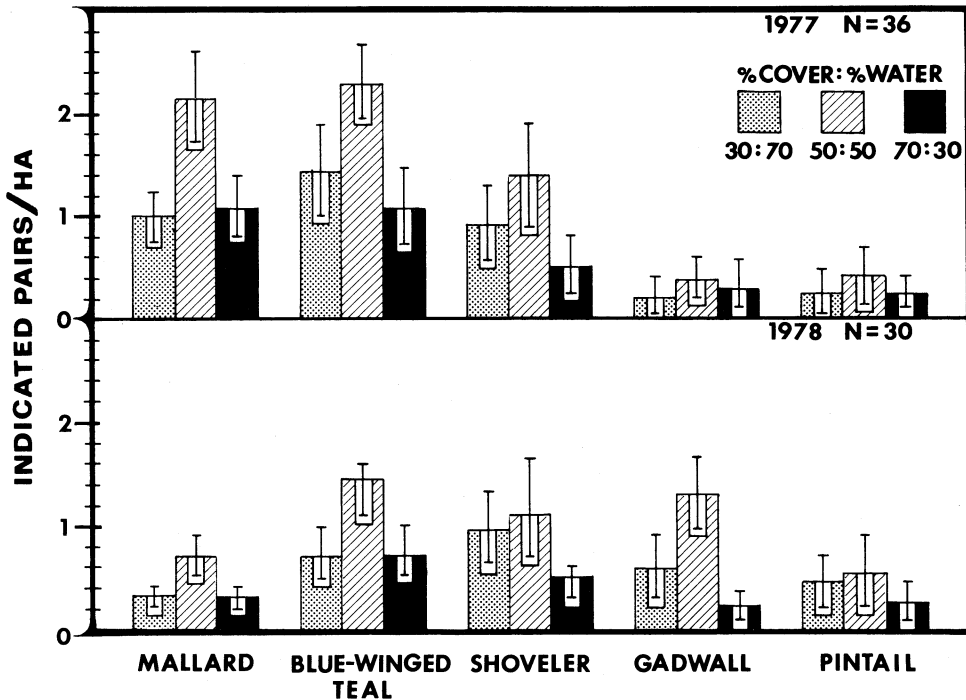


Fig. 2. Densities (\bar{x} and 95% CL) of pairs of dabbling ducks in 1-ha plots with different percentage ratios of cover to water, April-May, 1977 and 1978.

zero values) as mallards or blue-winged teal. Therefore, seasonal totals of species pair abundance were used to test the effects of habitat treatments by using 1-sample chi-square statistics.

Vegetation-to-water percentage ratios influenced dabbler pair densities more than basin treatments or survey times. The greatest pair density for all dabbler species in 1977 and 1978 occurred on 50:50 plots (Fig. 2). Generally, an equivalent or greater density of pairs was associated with 30:70 plots compared to 70:30 plots. Mallards and blue-winged teal responded similarly in 1977 and 1978 to treatment levels of vegetation and water. Higher ($P < 0.05$) pair densities for these species were recorded on 50:50 plots. The response was less clear for shovelers, gadwalls, and pintails.

Shoveler pair densities were higher ($P < 0.05$) in 1977 and 1978 on 50:50 plots compared to 70:30 plots, but no such difference ($P > 0.05$) existed between 50:50 and 30:70 plots in either year. Although gadwall and pintail pair densities were highest on 50:50 plots in both years, the difference was significant ($P < 0.05$) only for gadwalls in 1978.

Only blue-winged teal and pintail pair densities were greater ($P < 0.05$) on mowed than on rototilled plots in 1978. In 1977, there was no effect ($P > 0.05$) on pair densities of any species attributable to basin treatment.

Little variation in species pair densities was evident among morning, afternoon, and evening surveys. Differences did occur, however, in 1978 for blue-winged teal and pintails. That year fewer

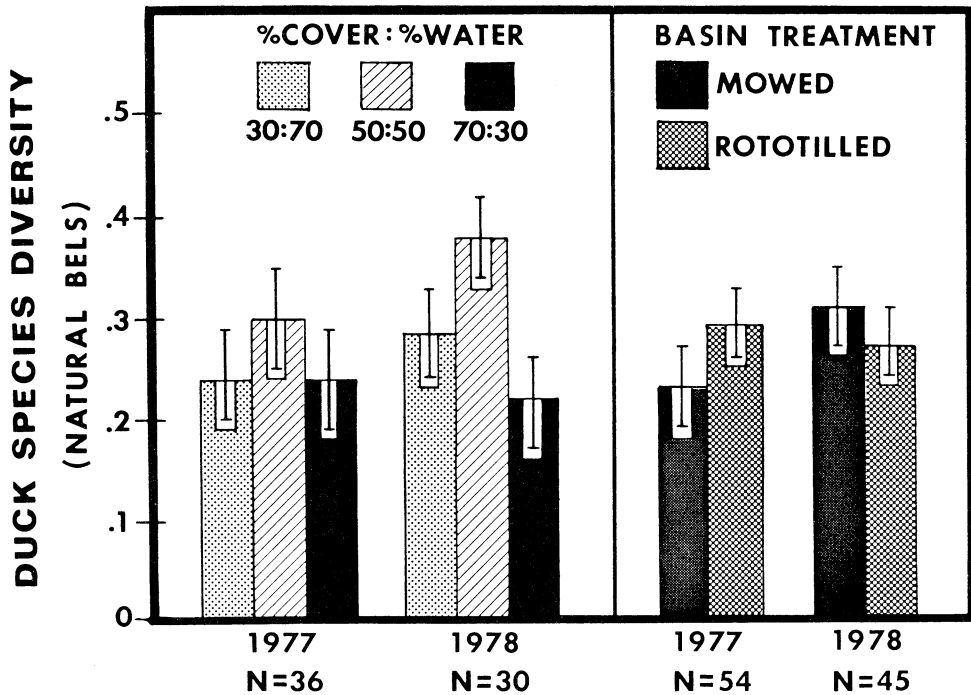


Fig. 3. Species diversity (H , \bar{x} , and 95% CL) of dabbling ducks observed in 1-ha plots with different percentage ratios of cover and water or different basin treatments, April–May, 1977 and 1978. Because diversity (H) was calculated using natural logarithms, the measurement unit of H is termed natural bel (Poole 1974:389).

($P < 0.05$) pairs of each species were observed during mornings compared to afternoons and evenings. Other researchers (Dzubin 1969, Jarvinen et al. 1977, Shields 1977) have recorded substantial diel variation in breeding-bird numbers.

Dabbling Species Diversity

Brillouin's formula was used to compute a value of dabbling duck species diversity for each plot per survey. ANOVA showed no effect ($P > 0.05$) on species diversity in 1977 due to vegetation-to-water percentage ratios, basin treatment, or time of survey. In 1978, the only factor contributing ($P < 0.05$) to differences in species diversity was the vegetation-to-water percentage ratio; diversity was highest ($P < 0.05$) on 50:50 plots (Fig. 3).

Pursuit Flights

The frequency of occurrence of pursuit flights in 1978 departed ($P < 0.005$) from expected frequencies for vegetation-to-water percentage ratios, as well as for basin treatments (Table 2). Fifty-seven percent of the flights originated from 50:50 plots as compared to 30 and 13% for 30:70 and 70:30 plots, respectively. Pursuit flights arose from mowed plots 74% of the time.

Aquatic Macroinvertebrates

Abundance, biomass, and number of families were selected as parameters in the evaluation of response of aquatic invertebrates to habitat treatments. ANOVA revealed no differences ($P > 0.05$) in mean invertebrate abundance, biomass,

Table 2. Aerial pursuits (*N*) of an intruding pair of ducks by a conspecific, territorial male.

Basin treatment	Cover:water ratio (%)			Totals ^a
	30:70	50:50	70:30	
Mowed	22 ^b	41	12	75
Rototilled	9	17	1	27
Totals ^a	31	58	13	102

^a Totals differ ($P < 0.005$) within columns and rows, which were tested separately (1-sample chi-square test).

^b Cell frequencies summed over 5 species: mallard 65/102 = 64%, pintail 17%, gadwall 12%, blue-winged teal 5%, shoveler 2%.

and number of families due to the vegetation-to-water percentage ratio in 1977 or 1978 (Table 3). Between years, estimates for mean abundance decreased, whereas biomass and number of families increased on treated areas.

Invertebrate abundance, biomass, and number of families varied among basin treatments within and between years (Table 4). Mean invertebrate abundance was greater ($P < 0.05$) on the control area than on mowed or rototilled areas in 1977. In 1978, mean abundance was highest on mowed plots, intermediate on

the control sites, and lowest on rototilled plots. Invertebrate numbers decreased between 1977 and 1978 on control, mowed, and rototilled areas. However, the decline was least dramatic on mowed plots (27%, $P > 0.05$) as compared to control (63%, $P < 0.05$) or rototilled (64%, $P < 0.05$) areas. Although the control area contained the greatest ($P < 0.05$) mean invertebrate biomass in 1977 and 1978, biomass estimates in 1978 decreased ($P < 0.05$) for the control and increased ($P < 0.05$) on mowed and rototilled plots. More ($P < 0.05$) families were represented in samples from mowed plots in 1977 and 1978 than from control and rototilled plots. There was an increase ($P < 0.05$) in the mean number of families between years on control and mowed areas, whereas family numbers on rototilled plots remained the same ($P > 0.05$).

Samples from the control area contained the fewest families in 1977 and 1978, and were dominated by midge larvae (Chironomidae) and water fleas

Table 3. Statistics (\bar{x} and 95% CL)^a for 3 parameters used to assess resource levels of aquatic invertebrates relative to percentage ratios of vegetation and water, 1977 and 1978.

Parameter	Year	Cover:water ratio ^b (%)		
		30:70 (<i>N</i> = 30)	50:50 (<i>N</i> = 40)	70:30 (<i>N</i> = 30)
Organisms/m ³	1977	8,381 (5,237–12,285)	9,938 (7,205–13,170)	12,190 (7,279–18,704)
	1978	5,364 (3,481–7,746)	6,788 (4,861–9,154)	4,765 (2,854–7,240)
Biomass, mg (dry weight)/m ³	1977	450 (398–607)	628 (478–993)	468 (403–670)
	1978	1,234 (843–1,760)	1,452 (1,003–2,057)	861 (518–1,348)
Families/m ³	1977	2.3 (1.8–3.0)	2.3 (1.8–2.8)	1.7 (1.4–2.0)
	1978	3.8 (3.2–4.4)	3.2 (2.5–3.8)	2.1 (1.6–2.7)

^a Means and 95% CL are back-transformed from a modified log transformation (Gill 1978:159).

^b No effect ($P > 0.05$) on any parameter in either year.

Table 4. Statistics (\bar{x} and 95% CL)^a for 3 parameters used to assess resource levels of aquatic invertebrates relative to basin treatments, 1977 and 1978.

Parameter	Year	Basin treatment		
		Control (N = 50)	Mowed (N = 50)	Rototilled (N = 50)
Organisms/m ³	1977	18,906 ^b (17,233–20,690)	11,336 ^c (8,331–14,901)	10,143 ^c (7,187–13,683)
	1978	6,993 ^b (5,525–8,558)	8,329 ^b (6,383–10,655)	3,685 ^c (2,548–5,030)
Biomass, mg (dry weight)/m ³	1977	11,161 ^b (9,506–13,116)	472 ^c (419–585)	550 ^c (444–811)
	1978	2,843 ^b (2,293–3,510)	909 ^c (717–1,138)	1,529 ^d (1,043–2,193)
Families/m ³	1977	1.2 ^b (1.1–1.3)	2.9 ^c (2.5–3.3)	1.5 ^d (1.3–1.8)
	1978	1.9 ^b (1.7–2.1)	4.6 ^c (4.3–5.0)	1.7 ^b (1.4–1.9)

^a Means and 95% CL are back-transformed from a modified log transformation (Gill 1978:159).

^{b-d} Row means with unlike superscripts differ ($P < 0.05$) by Bonferroni t statistics (Gill 1978:176).

(Daphnidae). A similar trend occurred on rototilled plots in 1977, but in 1978 midges and water fleas declined in occurrence and horsefly larvae (Tabanidae) became important (i.e., increased from 0 to 30% occurrence). The most diverse communities of invertebrates occurred on mowed plots in 1977 and 1978. There, water fleas, water mites (Hydrachnidae), and mosquito larvae (Culicidae) dominated in 1977 and 1978. In addition, predaceous diving beetle larvae (Dytiscidae) were important in 1977, as were soldier fly larvae (Stratomyiidae) and snails (Planorbidae and Physidae) in 1978. The abundance of soldier flies and snails increased ($P < 0.05$) between 1977 and 1978, whereas numbers of water boatmen (Corixidae), mosquitos, and diving beetles were similar ($P > 0.05$); these were the largest invertebrates encountered, with mean biomass estimates (dry weight \pm 95% CI) per organism of 2.16 \pm 0.61, 3.47 \pm 0.98, 3.86 \pm 1.08, 1.16 \pm 0.86, 1.26 \pm 0.82 mg, respectively (Kaminski 1979).

DISCUSSION

Drought

Dabbling duck pair use of the study area increased dramatically in the 1st year following habitat manipulations. The magnitude of response, however, was confounded by drought conditions that were geographically widespread in 1977 over southern Canada and much of the United States (Derksen and Eldridge 1980). High pair numbers in 1977 resulted from more pairs of mallards and blue-winged teal. This paralleled higher numbers for these species on the east Delta Marsh in 1977 as compared to 1976 or 1978 (R. M. Kaminski, unpubl. data). Greater pair numbers in 1977 may reflect a large-scale immigration of birds displaced from drought-deteriorated habitats. Influxes of presumed drought-displaced individuals and resultant increases in numbers of indicated pairs have been noted by Burgess et al. (1965), Dzubin and Gollop (1972), Jackson (1979), and Derksen and Eldridge (1980).

Hemi-marsh

Studying the effects of water-level perturbations on the dynamics of marsh vegetation and vertebrate populations, Weller and Spatcher (1965) and Weller and Fredrickson (1974) reported that avian abundance and species diversity were highest in several Iowa marshes during the hemi-marsh phase. Increased water levels and muskrat (*Ondatra zibethica*) populations characteristic of this phase produce an approximate 50:50 interspersed of emergent hydrophytes and open water. Our study empirically showed that dabbling duck breeding-pair densities and species diversity were greatest on 50:50 plots, which simulated a hemi-marsh configuration. However, what attributes of the hemi-marsh phase might relate to the responses observed in this study?

Bird species diversity in forest communities correlates positively with complexity of vertical habitat structure (MacArthur and MacArthur 1961). Structural features of marsh habitats, however, are for the most part restricted to the horizontal plane. The hemi-marsh phase represents a stage of marsh transition when horizontal habitat patchiness is high due to maximal interspersed of emergent vegetation and open water. Deviations from 50:50 cause a reduction in one of the structural components. Despite the fact that Wiens (1974) was unable to relate avifaunal abundance and diversity to habitat patchiness in grasslands, which are structurally similar to marshes, the findings of our study and others (Weller and Spatcher 1965, Weller and Fredrickson 1974, Möller 1975, Murkin 1979) strongly suggest that breeding dabbling duck abundance and species diversity are influenced in part by the amount of habitat patchiness.

Another established correlate of the hemi-marsh phase is high population levels of aquatic invertebrates. Voigts (1976) and Whitman (1974, 1976) recorded high numbers and temporally stable diversities of aquatic invertebrates when emergent vegetation and water were well interspersed in a marsh and in several impoundments, respectively. Similarly, Reinecke (1977) observed the greatest abundance and biomass of invertebrates in 3- to 5-year-old beaver ponds that contained plentiful amounts of emergents. Large quantities of emergent litter enter the water medium during the hemi-marsh phase through fragmentation, toppling, and muskrat activity (Davis and van der Valk 1978), and provide a detrital substrate that sustains high invertebrate populations. In our study, invertebrate abundance, biomass, and number of families were unaffected by vegetation:water ratios. Each year the plots were inundated for approximately 2 months, and then the water was drawn down and the study terminated. Visually there was little structural difference between manipulated and unmanipulated areas by late June of each year. Perhaps the plots did not retain their vegetation-water configuration long enough each year to manifest structural and/or functional effects on invertebrate faunas. Wetlands that undergo natural or artificially imposed successional changes of longer duration exhibit definite phase-related fluctuations in invertebrate populations. Breeding dabbling ducks may use abundant vegetation-water interspersed as a proximate cue to habitats rich in aquatic invertebrates. The greater pair densities and species diversity of dabblers on 50:50 plots could possibly reflect this.

An alternative and more simplistic hypothesis would be that the high dabbler

abundance and diversity on 50:50 plots were merely correlates of more available water area and/or openings per plot. If this were true, a greater response to plots with 30% vegetation and 70% water should have occurred unless social constraints precluded a more complete use of these. In 1978, social interactions among conspecifics, at least, seemingly did not limit pair density on 30:70 and 70:30 plots as much as on 50:50 plots, because significantly more pursuit flights originated from the latter.

The dabbling pairs on 30:70 and 70:30 plots might represent initial invaders or were displaced from 50:50 plots. Fretwell and Lucas (1969) hypothesized that as population density increases on preferred habitats, density-dependent effects should render suboptimal habitats equally suitable in terms of fitness prospects.

Basin Treatment

With the exception of blue-winged teal and pintails in 1978, basin treatment did not influence dabbling pair densities. The acquisition of space by breeding dabbling ducks possibly was more important than resource levels of aquatic invertebrates, which were affected by basin treatment. The greater pair densities of blue-winged teal and pintails on mowed areas in 1978 were probably related to the abundance of snails (primarily Planorbidae) on those plots. Breeding blue-winged teal (Dirschl 1969, Swanson et al. 1974) and pintails (Krapu 1974) forage preferentially on snails when available.

Basin treatments had a striking effect on resource levels of aquatic invertebrates. Invertebrate abundance, biomass, and number of families differed among control, mowed, and rototilled areas in 1977 and 1978. We recognize that these differences may be confounded by the

use of a different sampling device on mowed plots than on control and rototilled areas. Both sampling devices (modified Gerking sampler and the corer) enclosed a volume of water from surface to substrate and captured benthos and nekton. Thus, we assumed that the samplers functioned similarly in extracting invertebrates from the environment.

The majority of invertebrate families, irrespective of collection site, could be generally classed as detritivores with "collector" or "gatherer" foraging mechanisms (Cummins 1973, Merritt and Cummins 1978). Between years, invertebrate abundance, biomass, and number of families fluctuated in a manner typical of the dynamic nature of aquatic invertebrate populations (Swanson and Meyer 1977); however, the percentage changes in abundance and biomass were least on mowed plots. Furthermore, mowed plots contained the largest number of families of invertebrates and a preponderance of large-sized organisms (i.e., >1 mg [dry weight]/organism). This concurs with observations of Swanson et al. (1974) for seasonally flooded wetlands, which are structurally and functionally similar to the mowed plots of this study. Rototilled basins were intermediate and control areas were lowest in invertebrate faunal diversity and numbers of large organisms, probably because these basins were depauperate in detritus. The rich community of invertebrates in mowed basins was attributed to the abundance of decomposing detritus that also provided an additional structural dimension for invertebrate habitation. Energy and nutrients are contained in detritus, and microbes anabolize these constituents during decomposition. Microorganisms that colonize detritus form an important food source for aquatic invertebrates (Swanson et al. 1974, Berrie 1976, Swan-

son and Meyer 1977), which in turn are exploited by breeding dabbling ducks (Swanson et al. 1979).

Space and Food

Significantly more dabbler pursuit flights arose from 50:50 plots and mowed areas in 1978. A possible explanation for the greater occurrence of pursuit flights from 50:50 plots is that more dabbler pairs were initially attracted to these plots because of their hemi-marsh configuration, and subsequently were evicted by a male conspecific that defended the area. The confounding effects of habitat structure and the conspecific's presence, as potential attractants, cannot be separated.

Kaminski (1979) suggested that mowed areas may have been superior feeding patches for dabblers in 1978 because those areas harbored an abundance of large-sized aquatic invertebrates. Theoretically, it would be advantageous for dabblers to prey preferentially on abundant large invertebrates to satisfy dietary requirements as efficiently as possible. This may have been reflected by the greater establishment of defended areas within mowed plots in 1978. Although Patterson (1976) concluded that only available water influences the dispersion of breeding dabbling duck pairs, more research is needed to assay the relative importance of space and food on habitat selection and subsequent productivity of dabbling duck pairs.

MANAGEMENT RECOMMENDATIONS

Wetland areas in North America are diminishing at an alarming rate owing to competing demands for space from agriculture, industrialization, and urbanization. Preservation, restoration, development, and maintenance of wetlands are needed urgently if continental waterfowl

populations are not to be jeopardized. Results from our study imply habitat prescriptions that are especially appropriate for wetlands that have water-level control. Where these regulating capabilities are lacking and cannot be provided, the only recourse may be wetland preservation and dependence on natural hydrologic cycles.

Interspersion of emergent vegetation and water is 1 determinant of density and species diversity of breeding dabbling ducks. The response is greatest where vegetation and water are equally abundant in an interspersed pattern. Although indicated-pair densities and species diversities would predictably be highest during years of hemi-marsh conditions, consistently high nest densities and greater annual production need not ensue. In years of widespread drought, for example, pair densities could be high in areas where water persists, due to natural homing and immigration of drought-displaced individuals, but nesting densities and reproductive output might be low (e.g., Mayhew 1955, Derksen and Eldridge 1980). Waterfowl seemingly exhibit a temporally dynamic reproductive strategy (Nichols et al. 1976); some individuals apparently withhold reproduction (Dzubin and Gollop 1972) in drought years, whereas others immigrate to areas and breed (Giroux 1979). To evaluate fully the impact of habitat manipulations, yearly monitoring of waterfowl production should be concurrent with the manipulations.

Where water-level management is feasible, the most economical and efficient way to produce a hemi-marsh is through a drawdown. Complete dewatering of wetlands in the "degenerating" or "lake" marsh phases (van der Valk and Davis 1978) stimulates revegetation of the open basin. Interspersion of emergent vegetation and water then results from increas-

ing water levels and muskrat activity. Fragmentation and decomposition, especially of moist-soil plants, proceed rapidly during this period, because of their intolerance to water and their lower fiber content compared to more robust emergents like cattail and bulrush (*Scirpus* spp.) (Godshalk and Wetzel 1978); the accretion and decomposition of detritus cause invertebrate populations to temporarily flourish. Intervals between drawdowns should not exceed 5 years (Harris and Marshall 1963, Whitman 1974), so that detrital introductions remain substantial; however local vegetative responses may modify drawdown frequency. Abundance and biomass of invertebrates are much reduced in older-aged impoundments owing to dynamic processes (decomposition, soil-water chemical interactions, nutrient cycling, etc.); the interactive effects of these factors are not clearly understood. Additional guidelines for effective water-level management have been reviewed by Bellrose and Low (1978) and Weller (1978).

Mowing of vegetation, following a drawdown or over ice prior to significant snow accumulation, is an expedient means of creating openings in emergents as well as accelerating the fragmentation of detritus. Submergence of cattail stubble during subsequent growing seasons retards regrowth (Weller 1975, Murkin 1979). Presumably the water impedes oxygen transfer to the rhizome system, a storage depot for carbohydrates vital to initial growth in the spring (Linde et al. 1976). A random or uniform dispersion of openings should be better than clumping openings, which might overly aggregate breeding birds. The number of openings necessary to achieve a 50:50 ratio of vegetation and water depends on their size. Responses by marsh birds to size of openings have not been adequately

tested but appear to vary according to specific distance requirements for taking flight (Weller 1975). Observations from our study indicate that dabblers, divers (*Aythya* spp., *Oxyura jamaicensis*), and coots (*Fulica americana*) could become airborne on the 0.1-ha circles. An alternative and perhaps equally suitable technique for creating openings would be to mow vegetation in sinuous strips. This results in more edge than linear strips and would reduce visual encounters between conspecific pairs.

Rototilling is not recommended for creating openings in dense stands of emergents. It is mechanically difficult and 1 treatment does not inhibit plant regeneration significantly more than mowing. However, rototilling basins of wetland meadows and moist-soil units scarifies the substrate and encourages pioneering by desirable moist-soil plants (Taylor 1977; P. Ward, pers. commun.).

Fire as a tool to create openings in marsh emergents has been little studied (Ward 1968). Detailed investigations of its effects on marsh flora and fauna are necessary before implementation.

Current knowledge about chemical, physical, and biological influences on marsh ecosystems is meager. An interdisciplinary approach integrating the expertise of wildlife ecologists, botanists, limnologists, entomologists, and hydrologists should produce a more comprehensive understanding of the interrelationships among biotic and abiotic components of wetland ecosystems, and aid in devising proper wetland management practices (Weller 1978:280).

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