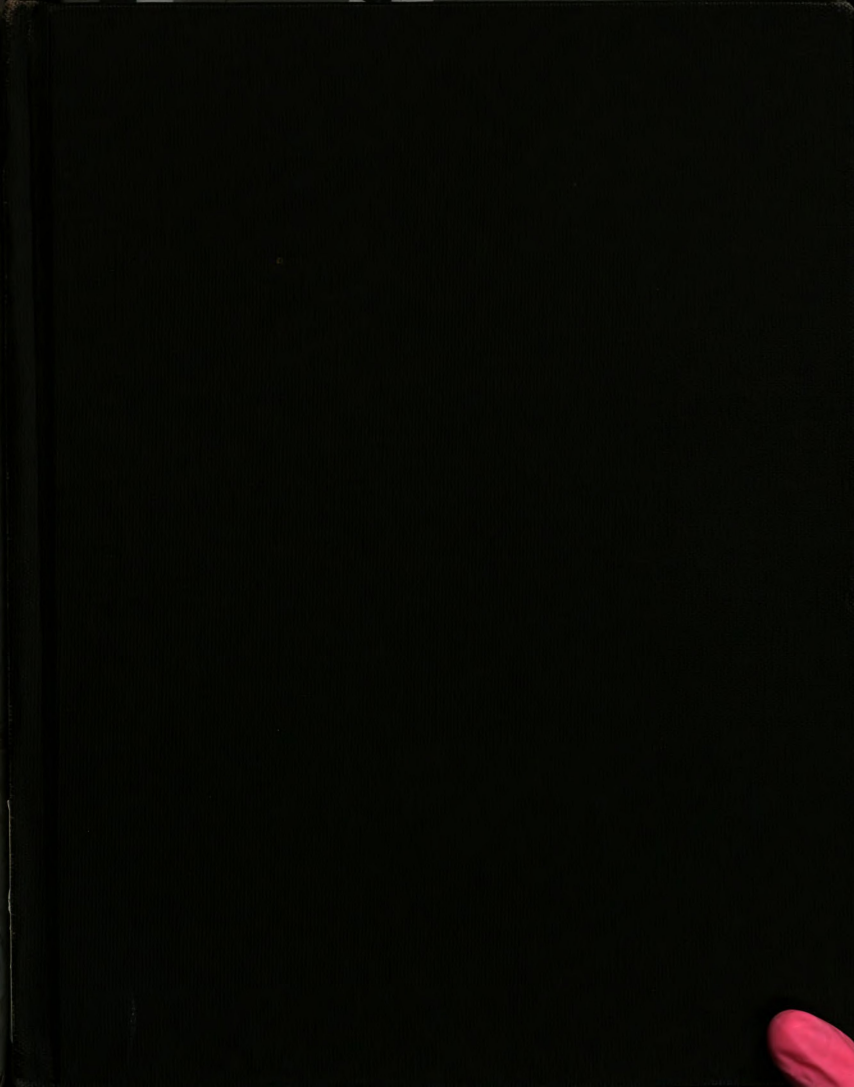






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DABBLING DUCK AND AQUATIC INVERTEBRATE RESPONSES

TO MANIPULATED WETLAND HABITAT

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Richard M. Kaminski

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Ph.D. degree in Wildlife


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DABBING DUCK AND AQUATIC INVERTEBRATE RESPONSES
TO MANIPULATED WETLAND HABITAT

By

Richard M. Kaminski

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

A 2-year study was conducted on a 33-ha impoundment in the Delta Marsh, south-central Manitoba (50°11'N, 98°19'W), to test the effects of manipulations of emergent hydrophytes and basin substrate on several parameters for breeding dabbling ducks (Anatini) and aquatic invertebrates. Replicate square plots (1 ha) were established which provided one of 3 areal percentage ratios of emergent vegetation to open water (30:70, 50:50, or 70:30), and one of 2 basin treatments (mowed vegetation or scarification by rototilling). Between years, numbers of mallard (Anas platyrhynchos) and blue-winged teal (A. discors) pairs declined significantly while pair numbers of northern shoveler (A. clypeata), gadwall (A. strepera), and pintail (A. acuta) were comparable. Weather was not confounded with habitat treatments on species-pair numbers in 1977 or 1978. The greatest density and species diversity of dabbling pairs occurred on 50:50 plots in both years. The response appeared linked to an interaction between habitat structural complexity and its indirect effects on aquatic invertebrate population levels. Only blue-winged teal and pintail pair densities in 1978 were greater on mowed than on rototilled areas, and there was no difference in dabbling species diversity between mowed and rototilled areas within years. Significantly more pursuit flights arose from 50:50 plots and mowed areas compared to alternative treatment types, suggesting correlates of territorial site

selection and spatial dispersion of dabbling duck pairs. Discriminant function analysis for each dabbling species showed that mowed, rototilled, and untreated areas differed based on the percentage occurrence of 6 activity categories; however, no activities were specific to treated or control areas. Composition and resource levels (abundance, biomass, and number of taxa) of aquatic invertebrate communities varied within and between years in response to basin treatments. It was argued that breeding dabbling ducks gauge their foraging effort by the 'profitability' of encountered feeding patches, perhaps an adaptive tactic for exploiting fluctuating invertebrate populations in wetlands. Implications for habitat management and future research needs were outlined.

*In memory of my mother,
who was summoned well before her time.*

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Special recognition is given to Loretta, my wife, for enduring the life style of a man who prefers wearing hip boots over oxfords and for expertly typing this manuscript. Lastly but in no way least, I gratefully thank my parents, Al and Jeanne, for their constant concern for Loretta and I.

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INTRODUCTION

The interaction of proximate and ultimate factors (Hilden 1965) continues to intrigue ecologists who study avian habitat selection. Since the pioneering work by Beecher (1942) and Svårdson (1949), significant theoretical advances into the possible causes of habitat selection have emerged (Fretwell and Lucas 1969, Southwood 1977, MacArthur and Levins 1964, Rosenzweig 1974, Bryant 1973). Theory predicts that animals should select habitats where fitness prospects outweigh costs of exploitation. Unfortunately, the hypothesis remains untested.

Habitat selection in birds is seemingly guided by instinctive and experiential influences from the physical and/or social environment (Hilden 1965). Numerous efforts 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 (Klopfer 1963, Partridge 1974). The

experiment described here was planned to investigate habitat use by breeding dabbling ducks under field conditions. The majority of literature on this subject originated from studies conducted in pothole habitats of the United States and Canada. Thus, habitat use by breeding dabbling ducks on large marshes is not well known. Weller and Spatcher (1965) and Weller and Fredrickson (1974), studying glacial marshes in Iowa, showed that avian abundance and diversity was highest during years when emergent hydrophytes and open water covered approximately equal areas in a highly interspersed pattern. They termed this stage of succession the 'hemi-marsh' phase. Inspired by their work, an experiment was conducted on the Delta Marsh, Manitoba to test the hypothesis that there would be unequal responses in density and species diversity of breeding dabbling ducks to differing levels of emergent vegetation and open water. Specifically, 3 areal percentage ratios of emergent vegetation to water were artificially created for experimentation: (1) 30:70, (2) 50:50 (simulated hemi-marsh configuration), and (3) 70:30. In addition, dabbler activity and resource levels of aquatic invertebrates were measured relative to habitat treatments. Dabbler species under investigation were mallard, blue-winged teal, northern shoveler, gadwall, and pintail; the most common dabbling ducks breeding on the Delta Marsh (Sowls 1955).

STUDY AREA, METHODS, AND MATERIALS

Study Area

The study was conducted on a 33-ha seasonally flooded emergent habitat (Cowardin et al. 1976) 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).

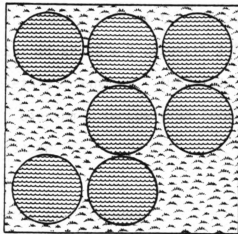
A wooded beach ridge, separating Lake Manitoba from the Delta Marsh, formed the northern boundary of the study area. In March 1977, an earthen dike was constructed around the southern reach of the area so water levels could be controlled. Originally, an unbroken, dense stand of emergent hydrophytes existed across the area. Thus, a natural interspersions of vegetation and open water did not confound experimental levels of interspersions. Areal percentages of predominant flora were white-top grass (Scolochloa festucacea) (60 percent), cane (Phragmites australis) (30 percent), cattail (Typha spp.) (5 percent), and sedge (Carex spp.) (5 percent). The soil was histisol (Buckman and Brady 1969).

Habitat Manipulations

In July 1976, 18 square plots (1 ha) were established by 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 heavy machinery.

A diagrammatic example of plot design is illustrated in Figure 1. Each of the 18 plots provided one of 3 areal percentage ratios of emergent vegetation to open water (30:70, 50:50, or 70:30), and one of 2 basin treatments (mowed vegetation or scarification by rototilling). This furnished 3 replicates of 6 treatment combinations which were randomly assigned to plots. Areas with mowed vegetation or rototilled substrates mimicked basins of seasonally flooded emergent or tilled wetlands, respectively. Vegetation was mowed with a tractor-drawn rotary mower in 3, 5, or 7 0.1-ha circles to create open-water areas (upon inundation) of 30, 50, or 70 percent, respectively per 1-ha plot (Figure 1). The centers of circles were randomly located from 9 possible points per plot to minimize positional bias. Mowed vegetation was left lying where mowing was the specified treatment. Before rototilling designated circles in 1976, it was necessary to remove the litter. This was done by consolidating litter into piles with a side-delivery hay rake and then burning them. Burning prior to rototilling was not necessary in 1977. Concentric paths were followed while mowing and rototilling to evenly distribute the treatments' effect. Plot treatments of 1976 were repeated in August 1977 in preparation for the 1978 season.

Figure 1. A diagrammatic example of experimental plots.

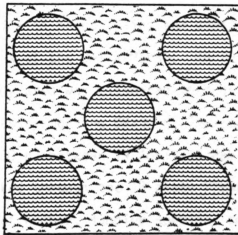


30:70

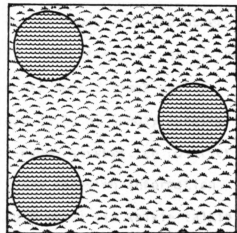
LEGEND



% COVER:% WATER
SQUARES 1HA
CIRCLES 0.1HA



50:50



70:30

The impoundment was inundated between 11-19 April 1977-78 by pumping water from the Delta Marsh. This was approximately 2 weeks before peak numbers of dabbling duck pairs were observed on the study area. Water was present in all circles and there was no significant difference ($P > 0.05$) in weekly sampled water depths among 5 randomly chosen sites scattered throughout the impoundment. Water depth was maintained at 32 ± 3 cm until 3-7 June 1977-78 when water levels were completely drawdown. The study was terminated on 30 May 1977-78 to avoid biasing interspersions levels and observations from growing vegetation.

Breeding Pair Surveys

Six morning helicopter (Bell 47G-4A) surveys were conducted (12 April-21 June 1976) to estimate pretreatment numbers of dabblers indicated pairs (pairs and single males) 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 (Tuesday morning 07:30 h, Thursday afternoon 15:00 h, Sunday evening 18:30 h) between 19 April-28 May. During ground surveys, an observer walked through the 18 plots flushing ducks and relaying information (plot number, dabbler species, pair or single male) via walkie talkie to an assistant in an elevated blind who visually followed (using binoculars) the flight route of flushed birds. The observer was informed of previously counted birds that alighted on plots yet to be surveyed to prevent duplicating pair counts.

Ground count data were used to compute Brillouin's index of species diversity (H). The index, taken from information theory, involves

species richness and relative abundance (Poole 1974). It is appropriate when individuals of a finite number of populations are identified and enumerated from nonrandomly selected samples (Poole 1974); a situation applicable to the present 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 , $i = 1, 2, 3, \dots, s$.

Dabbler Activity

Activities of unmarked pair members and single male dabbling ducks were observed to compare activity patterns between mowed, rototilled, and control areas (i.e., 2 untreated bays of the Delta Marsh adjacent to the impoundment). Concurrent observations were made by 2 people using spotting scopes (15-60X) between 19 April-30 May 1977-78. Each person continuously scanned a separate section of the study area for 2-h periods from an elevated blind and recorded the current activity of all visible dabblers according to species, male/female pair member or single male, and basin treatment (control, mowed, or rototilled). Activities were categorized as foraging, resting, locomotor, comfort movements, alert, or courtship displays. Randomly selected starting hours for observation sessions were 06:00-10:00 h and 13:00-15:00 h; evening observations began at 18:30 or 19:00 h. A total of 292 and 204 man hours were spent observing in 1977 and 1978, respectively.

While observing 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 either observing the initiation of flights or the return of the defending male to a specific location. Observers compared notes on flight initiation times, directions, and subsequent return locations to prevent duplication.

Aquatic Invertebrates

Samples of aquatic invertebrates were collected weekly throughout the 1977 and 1978 study periods. One sample was collected from the approximate center of 10 randomly selected mowed and rototilled 0.1-ha circles and from 10 randomly chosen open-water sites within one of the control bays. Depth of water at each site was measured. A single-core sampler (50 cm plastic pipe, 8.5 cm in diameter), as illustrated by Merritt and Cummins (1978, Figure 3.11), was used to sample rototilled circles and control sites. The corer did not function on mowed circles because of interference with litter. Instead a sampler, modified after Gerking (1957), consisting of a steel-rod frame (21 X 52 X 107 cm) covered with nylon netting (0.5 mm apertures) was used to sample mowed plots. In the lab, invertebrates were identified to family using Merritt and Cummins (1978) and Pennak (1953), counted, and a sample of each taxa was oven dried (105°C) for 24 h (Cummins and Wuycheck 1971), and then weighed on a Mettler H-54 balance. Samples taken with the corer were combined with a liberal volume of sucrose solution (1 kg sugar/2 l water) which floated invertebrates to the surface for ease of sorting (Flannagan 1973).

Analytic Procedures

Statistical analyses followed Gill (1978), Nie et al. (1970), or Sokal and Rohlf (1969). Data sets not meeting assumptions of analysis of variance were transformed by either square root or log procedures (Gill 1978). Variation around estimated mean values was expressed as either 1 standard error or 95 percent confidence limits.

RESULTS

Temporal Variation in Pair Numbers

Although the study area was naturally inundated during the pretreatment period of 1976, few indicated pairs (hereinafter called pairs) of dabbling ducks were observed from the helicopter. An average of 2 pairs per survey ($n = 6$) were observed in 1976 contrasted with averages of 73 ($n = 18$) and 43 ($n = 15$) pairs for treatment period ground surveys of 1977 and 1978, respectively.

Early returning (4-14 April 1977-78) mallards and pintails initially used portions of the study area where 'sheet' water accumulated. Inundation of the area was delayed until 11-19 April 1977-78, because ice conditions on the Delta Marsh prevented earlier flooding. As flooding progressed, pairs and groups of dabbling ducks gradually moved onto the unit. Approximately equal numbers of pairs were observed during the first week of each year (Figure 2). Mean pair numbers for all dabbling species combined peaked at 97 ± 3 (S.E., $n = 3$) and 53 ± 10 (S.E., $n = 3$) between 1-7 May 1977 and 1978, respectively. By late May, mean pair numbers declined to approximately 40 percent of peak numbers. Differences between years in mean numbers of pairs during May (Figure 2) were attributed to marked changes in population levels of mallards and blue-winged teal (Table 1). Mallard and blue-winged teal mean pair numbers decreased by 68 and 44 percent, respectively between 1977 and

Figure 2. Weekly variation in mean pair numbers (S.E.) for all dabbling duck species combined, 1977-78.

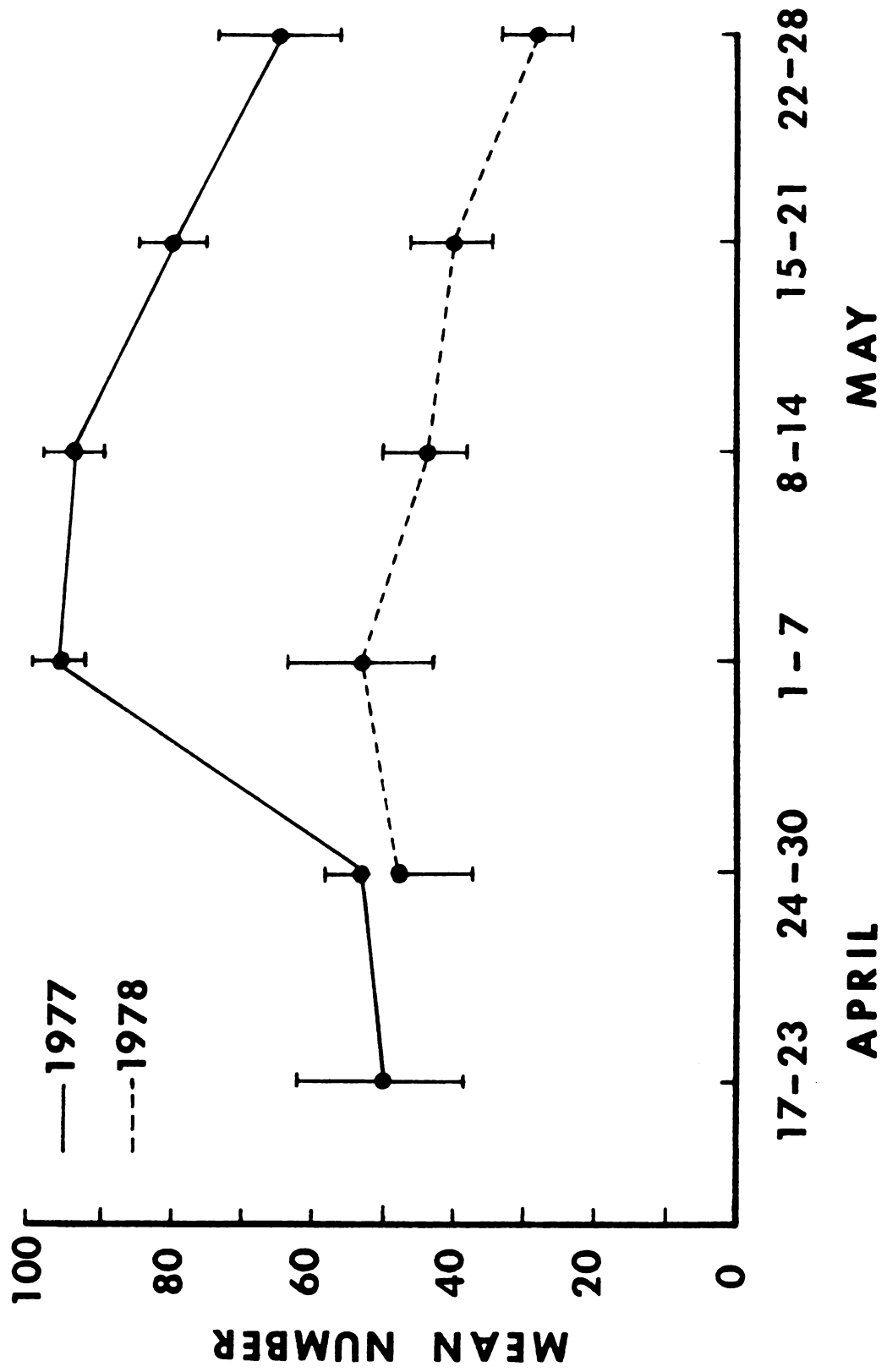


Table 1. Mean number ($\pm$ S.E.) of species pairs per ground survey, 1977-78.

Species ^a	Year	
	1977 (n=18)	1978 (n=15)
Mallard	28 ± 2 ^b	9 ± 1 ^c
Blue-winged teal	34 ± 4 ^b	19 ± 3 ^c
Shoveler	7 ± 1 ^b	6 ± 1 ^b
Gadwall	3 ± 1 ^b	5 ± 1 ^b
Pintail	2 ± 1 ^b	3 ± 1 ^b
Grand mean	73 ± 5 ^b	43 ± 4 ^c

^aSpecies means without the same superscript are different (P < 0.05) by Mann-Whitney U test.

1978 while shoveler, gadwall, and pintail pair numbers were similar.

Weather

Daily weather records were obtained from the University of Manitoba Field Station located approximately 6 km due west of the study area. Stepwise multiple regression was used to test the relationship between 5 weather variables (ambient temperature, solar index, wind speed and direction, presence or absence of rain) and the number of pairs of a dabbling species per census. None of the variables were related ($P > 0.05$) to species pair numbers in 1977 ($n = 18$) or 1978 ($n = 15$), suggesting that weather and habitat treatments were not confounded.

Pair Densities and Habitat Treatments

The effects of habitat treatments (percentage ratios of vegetation to water and basin treatments) and survey time (morning, afternoon, or evening) on weekly variation in mallard and blue-winged teal pair densities were analyzed with a 3-factorial analysis of variance. These species were abundant both years; few (< 10 percent) replicates per treatment combination had zero values. Designed comparisons among means of significant factors were made with the Bonferroni t-statistic (Gill 1978). Shoveler, gadwall, and pintail pairs were less numerous (37-75 percent of the replicates had zero values); therefore, factor effects on seasonal pooled totals were tested using chi-square one-sample statistics.

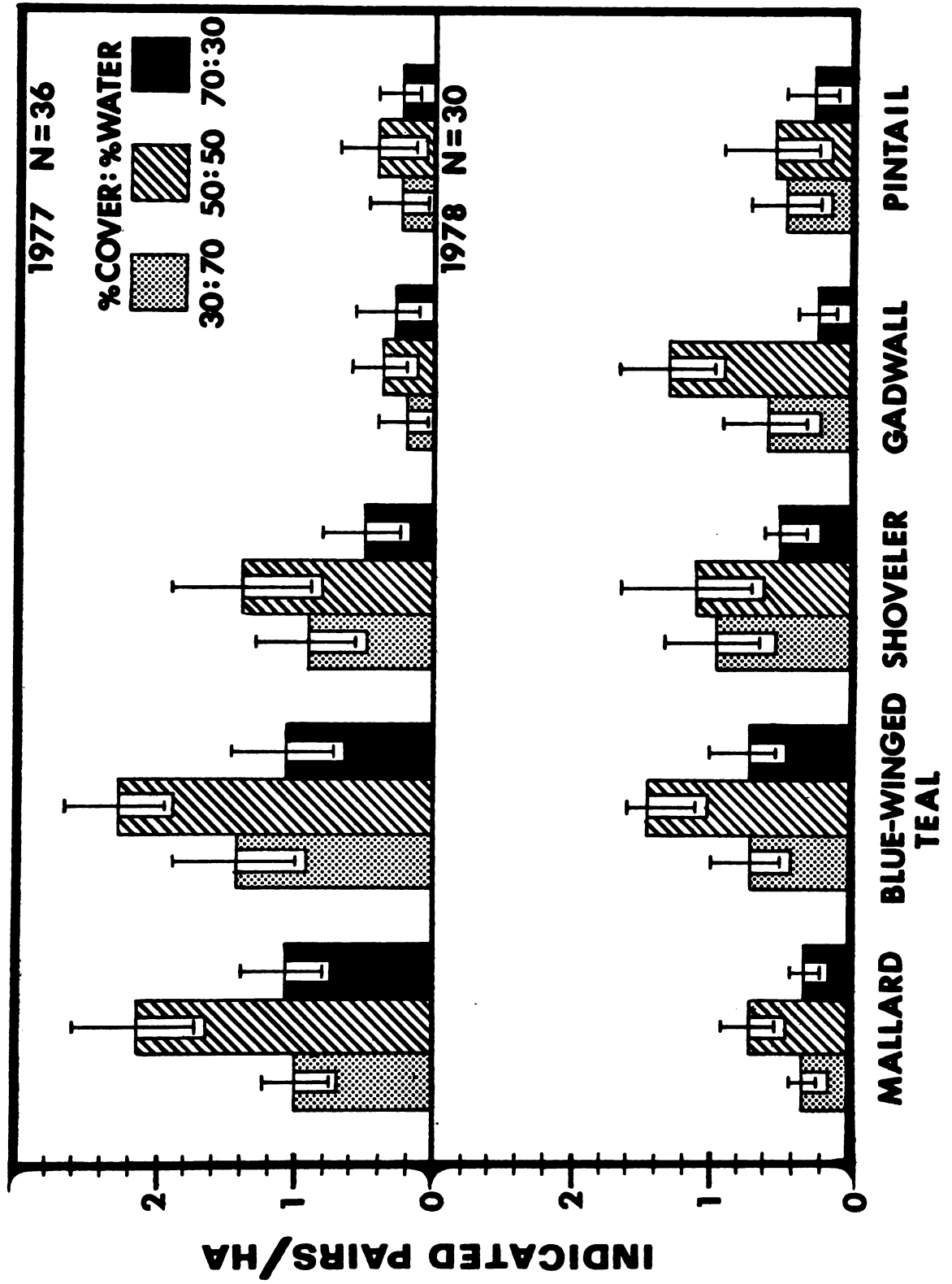
Percentage ratios of vegetation to water influenced dabbling pair densities more than basin treatment or survey time. The greatest pair

density for all dabbling species in 1977 and 1978 occurred on 50:50 plots (Figure 3). 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. Significantly 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 significantly 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.

In 1977 and 1978, there was no significant effect ($P > 0.05$) on mallard pair densities attributable to basin treatment. The same was true for blue-winged teal in 1977, shovelers in 1977-78, gadwalls in 1977-78, and pintails in 1977. Blue-winged teal and pintail pair densities were greater ($P < 0.05$) on mowed than on rototilled plots in 1978.

Little variation in species pair densities was evident between morning, afternoon, and evening surveys. Differences did occur, however, in 1978 for blue-winged teal and pintails. That year significantly fewer ($P < 0.05$) pairs of each species were observed during mornings compared to afternoons and evenings. Other researchers (Dzubin 1969, Jarvinen et al. 1977, Shields 1977) have noted substantial diel variation in breeding bird numbers.

Figure 3. Mean (95% C.I.) pair densities of dabbling ducks by percentage ratio of vegetation to water, 1977-78.



Dabbler Species Diversity

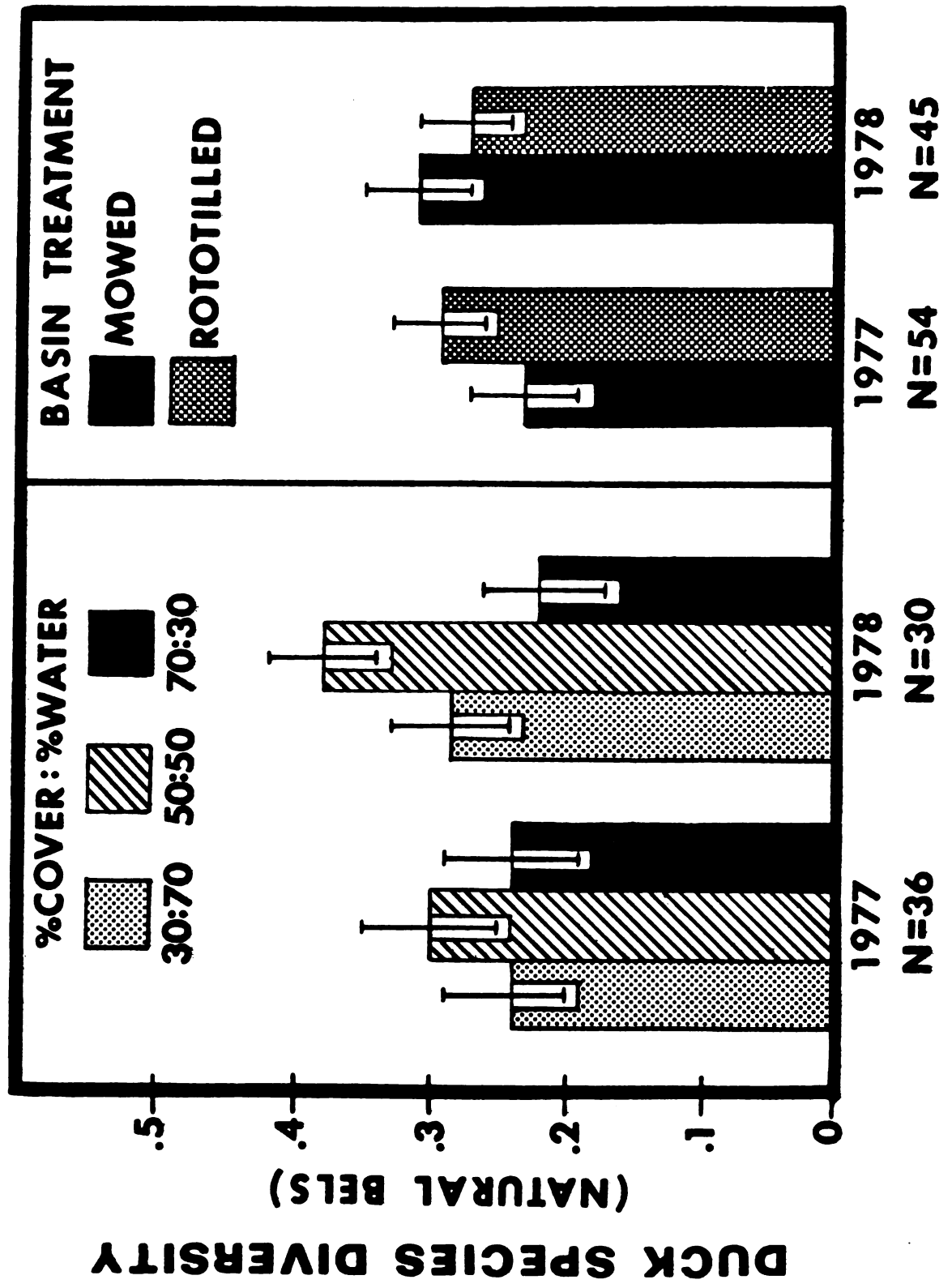
Although dabbler pairs were more abundant in 1977 than in 1978, the average species diversity per survey was 10 percent less ($P > 0.05$) in 1977. Analysis of variance revealed no significant effect ($P > 0.05$) on dabbler species diversity in 1977 due to percentage ratios of vegetation to water, basin treatment, or time of survey. In 1978, the only factor contributing significantly ($P < 0.05$) to differences in species diversity was the percentage ratio of vegetation to water (Figure 4). Species diversity was highest on 50:50 plots in both years, but only in 1978 was the difference significant ($P < 0.05$).

No pattern emerged in species diversity between 1977 and 1978 relative to basin treatments (Figure 4). Rototilled plots had a higher mean value for species diversity in 1977 whereas mowed plots did in 1978.

Dabbler Activity

Stepwise discriminant function analysis, a multi-variate analytical procedure (Nie et al. 1970), was used initially to test for differences between 3 groups (male/female pair members and single males) using the percentage occurrence of 6 activities (forage, rest, locomotor, comfort movements, alert, or courtship displays) as discriminating variables. A separate analysis was performed for each dabbler species within basin treatments and years. In 17 of 30 analyses a significant separation ($P < 0.05$) was detected (by Wilk's lambda criterion), but significance was usually (13 of 17) restricted to the first discriminant functions (2 possible). Overlap in the occurrence of activities between groups was reflected in the low percentage of cases correctly classified (32-61

Figure 4. Mean (95% C.I.) values of dabbling duck species diversity by percentage ratio of vegetation to water and basin treatment, 1977-78.



percent) by this analysis. For these reasons, data were pooled to the level of species.

Table 2 provides summary statistics for discriminant analyses now contrasting basin treatments as groups within species and years. In most cases, the first and second discriminant functions were highly significant indicating that the measured activities contained considerable discriminating power. It is important that the increased sample sizes, obtained by pooling data, accounted in part for the significant discriminations. Although both functions were usually significant, the percentage of cases correctly classified only ranged from 46-60 percent. This denoted substantial overlap in dabbling activities among basin treatments and prevented accurate prediction of group membership based on the measured variables.

The relative importance of a variable to a function was evaluated by the absolute value of the variable's standardized discriminant function coefficient (Table 2). Examination of the coefficients revealed that foraging activity was consistently important in separating groups in 1977 and 1978. Foraging and alert contributed significantly in the first functions for all species except mallards in 1977. In 1978, other variables combined with foraging to separate groups. Foraging was also important in the second functions, but its contribution was less than in the first. Since most of the discriminating information in foraging was extracted by the first functions, this was not a surprising result.

The mean percentage occurrence of activities by dabbling species and basin treatment is illustrated in Figures 5 and 6 for 1977 and 1978, respectively. In 1977 and 1978, dabblers were most frequently observed

Table 2. Summary statistics of discriminant function analyses contrasting basin treatments, using the percentage occurrence of 6 activities as discriminating variables.

		Standardized discriminant function coefficients ^{a,b} of activity variables															
		Function I (P<0.001)					Function II (P<0.02) ^c										
Year	Species	N of groups													% of cases correctly classified		
		Control	Mixed	Rototilled	Forage	Rest	Locomotor	Comfort	Alert	Court	Forage	Rest	Locomotor	Comfort		Alert	Court
1977	Mallard	177	144	146	1.3	0.5		0.3	1.1								53
	Blue-winged teal	198	175	196	-1.3	-0.3	0.2	-0.1	0.4	-0.9							56
	Shoveler	107	89	149	0.7		-0.6	0.8		0.8							46
	Gadwall	132	41	83	0.9		0.4	0.2	-0.8	0.6							57
	Pintail	70	48	48	1.1		0.3	0.1		1.0							57
1978	Mallard	92	84	79	1.0		-0.3	0.3		0.9	0.5						51
	Blue-winged teal	44	123	112	1.4	0.5		0.6	1.4								53
	Shoveler	24	88	56	-0.3	0.5	0.8	-1.4	-0.7	-1.1							55
	Gadwall	86	72	46	-1.0	-0.4	-0.5	0.1	-1.0								56
	Pintail	30	81	28	1.0	-0.4	0.1	0.1	0.1	1.0	-1.0						60

^a Absolute value of coefficient denotes a variable's contribution to the function.
^b Variables without a coefficient did not contribute (P>0.1) to the discrimination.
^c Function II not significant (P>0.4) for blue-winged teal and shovellers in 1977 and gadwall in 1978.

Figure 5. Mean (S.E.) percentage occurrence of activities by basin treatments (C = control, M = mowed, R = rototilled) and dabbling species, 1977 (t denotes trace, < 2%).

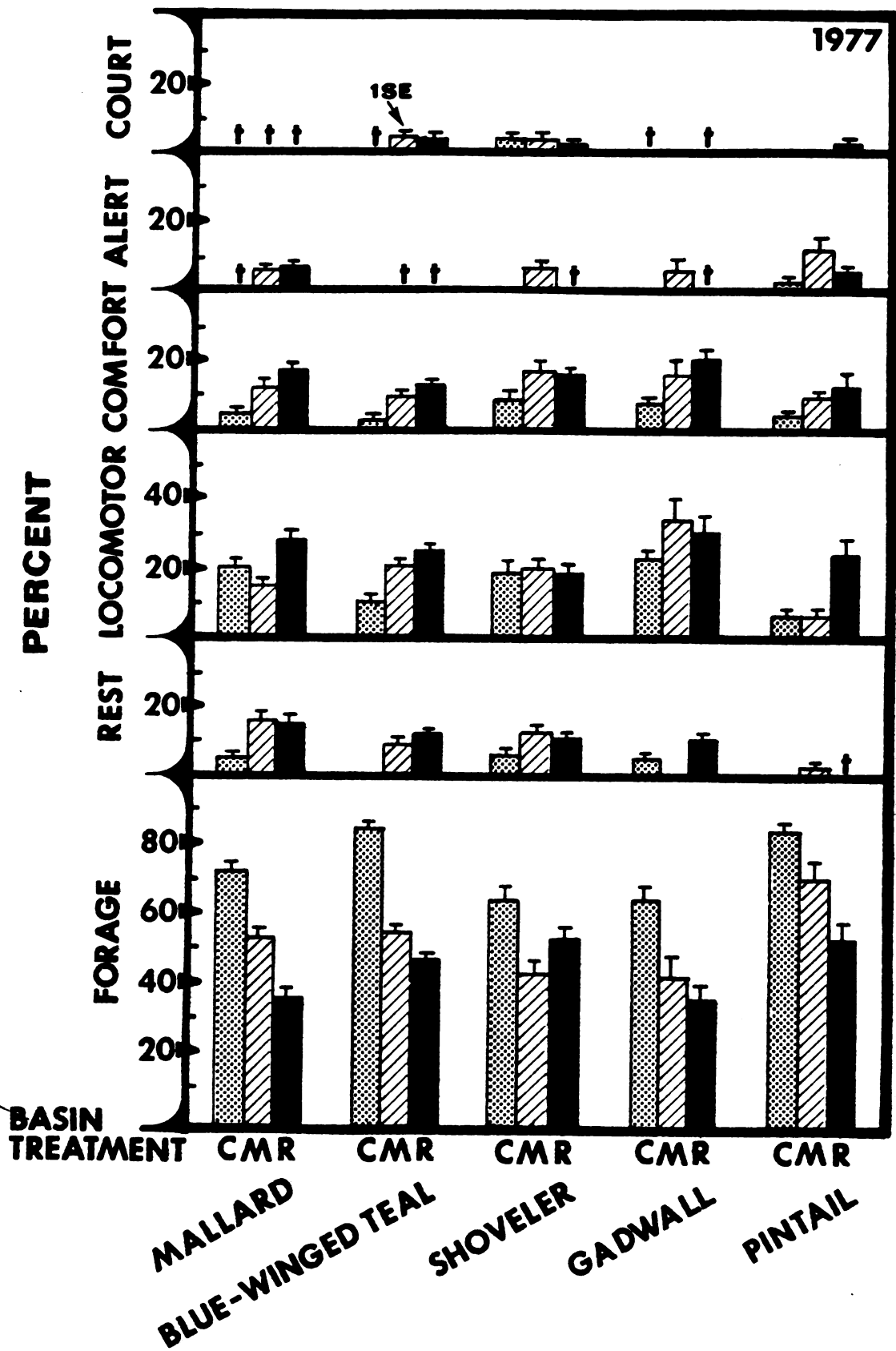
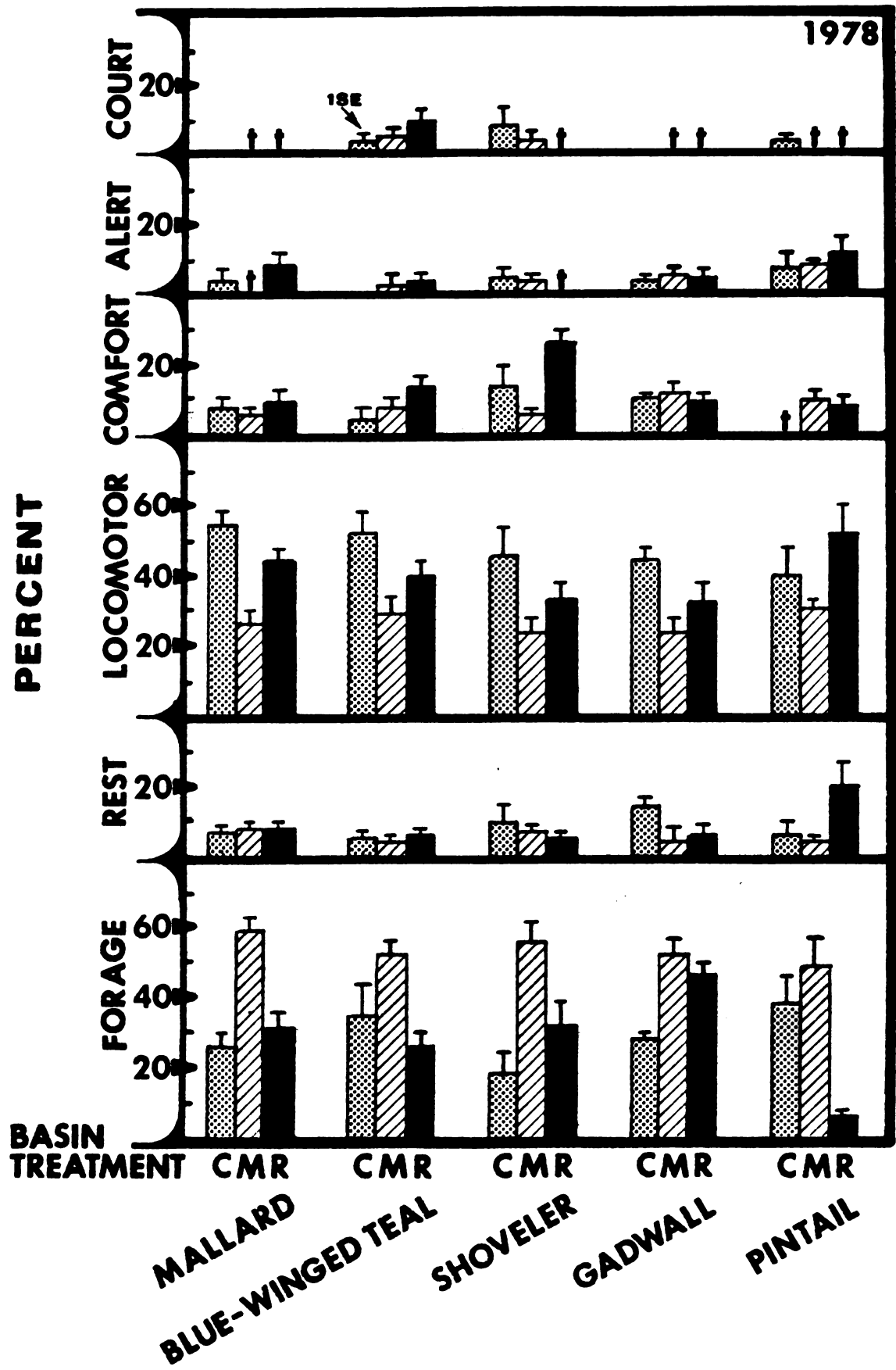


Figure 6. Mean (S.E.) percentage occurrence of activities by basin treatments (C = control, M = mowed, R = rototilled) and dabbling species, 1978 (t denotes trace, < 2%).



engaging in foraging and locomotor activities followed by comfort movements and resting behavior. Alert and courtship activity comprised only a minor percentage of the activities in both years. The percentage occurrence of comfort movements and resting activity varied less among basin treatments in comparison to foraging and locomotor. Mean percentage occurrence of foraging and locomotor activities were inversely related within basin treatments in 1977 ($r = -0.81$, $df = 13$, $P < 0.01$) and 1978 ($r = -0.86$, $df = 13$, $P < 0.01$). Foraging by all species occurred most frequently on the control area in 1977 (Figure 5) whereas its greatest occurrence in 1978 was on mowed plots (Figure 6). The occurrence of foraging on mowed plots for all dabblers combined did not change between 1977 (54 ± 5 percent) and 1978 (54 ± 2 percent). On control (75 ± 5 vs. 29 ± 4 percent) and rototilled (46 ± 3 vs. 29 ± 6 percent) areas, however, there was a significant decrease ($P < 0.05$) in foraging between 1977 and 1978.

Pursuit Flights

The frequency of occurrence of pursuit flights in 1978 by habitat treatment combination significantly ($P < 0.005$) departed from expected frequencies for percentage ratios of vegetation to water as well as for basin treatments (Table 3). Fifty-seven percent of the flights originated from 50:50 plots as compared to 30 and 13 percent for 30:70 and 70:30 plots, respectively. Pursuit flights arose from mowed plots 74 percent of the time.

Table 3. Frequency of occurrence of pursuit flights by habitat treatment combination, 1978.

Basin treatment ^a	% cover : % water ^a			Total
	30:70	50:50	70:30	
Mowed	22 ^b	41	12	75
Rototilled	9	17	1	27
Total	31	58	13	102

^aColumn and row totals differ ($P < 0.005$, one-sample Chi-square test).

^bCell frequencies are totals for 5 species (mallard = 64%, pintail = 17%, gadwall = 12%, blue-winged teal = 5%, shoveler = 2%).

Aquatic Invertebrates

Abundance, biomass, and number of taxa were selected as parameters to evaluate resource levels of aquatic invertebrates in response to habitat treatments. Analysis of variance showed no significant interaction ($P > 0.05$) between the factors, percentage of vegetation to water and basin treatment (mowed or rototilled), for any parameter in 1977 or 1978.

There were no differences ($P > 0.05$) in mean invertebrate abundance, biomass, and number of taxa due to the percentage of vegetation to water in 1977 or 1978 (Table 4). Between years, estimates for mean abundance decreased whereas biomass and number of taxa increased on manipulated areas.

Invertebrate abundance, biomass, and number of taxa varied between basin treatments within and among years (Table 5). Mean invertebrate abundance was significantly greater ($P < 0.05$) on the control area than on mowed or rototilled plots in 1977. In 1978, mean abundance was highest on mowed plots, intermediate on the control, 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 percent, $P > 0.05$) as compared to control (63 percent, $P < 0.05$) and rototilled (64 percent, $P < 0.05$) areas. Although the control area contained the greatest ($P < 0.05$) mean invertebrate biomass in 1977 and 1978, biomass estimates for the control decreased ($P < 0.05$) in 1978 and increased ($P < 0.05$) on mowed and rototilled plots. Significantly more ($P < 0.05$) invertebrate taxa were represented in samples from mowed plots in 1977 and 1978 compared to the alternate basin treatments. There was a significant ($P < 0.05$)

Table 4. Mean (95% C.I.) values for 3 parameters used to assess resource levels of aquatic invertebrates relative to percentage ratios of vegetation and water, 1977-78.

Parameter	Year	% cover : % water ^b		
		30:70 (n=30)	50:50 (n=40)	70:30 (n=30)
Number of organisms/m ³	1977	8,381 ^a (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	449.5 (397.5 - 607.0)	628.2 (477.6 - 993.1)	467.9 (402.7 - 670.1)
	1978	1,233.8 (842.5 - 1,760.1)	1,451.5 (1,002.5 - 2,056.5)	860.5 (518.1 - 1,347.9)
Number of taxa/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)

^aMeans and 95% confidence limits are back transformed from a modified log transformation (Bliss 1967).

^bNo significant effect ($P > 0.05$) on any parameter in either year.

Table 5. Mean (95% C.I.) values for 3 parameters used to assess resource levels of aquatic invertebrates relative to basin treatments, 1977-78.

Parameter	Year	Basin treatment ^{a,b}		
		Control (n=50)	Mowed (n=50)	Rototilled (n=50)
Number of 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	6,933 ^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	11,161.2 ^b (9,506.1 - 13,116.3)	472.0 ^c (418.9 - 584.8)	550.0 ^c (444.1 - 811.0)
	1978	2,843.0 ^b (2,293.2 - 3,509.9)	909.2 ^c (717.3 - 1,137.6)	1,529.4 ^d (1,043.0 - 2,193.2)
Number of taxa/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)

^aMeans and 95% confidence limits are back transformed from a modified log transformation (Bliss 1967).

^bParameter means without the same superscript are different (P<0.05) by Bonferroni t statistic (Gill 1978).

increase in the mean number of taxa between years on control and mowed areas while the number of taxa on rototilled plots remained the same ($P > 0.05$).

Variation between years in the percentage occurrence of aquatic invertebrate taxa by basin treatment, and their mean biomass (dry weight) per organism is presented in Table 6. Samples from the control area contained the fewest taxa in 1977 and 1978, being dominated by midges (Chironomidae) and water fleas (Daphnidae). The same was true for rototilled plots in 1977, but in 1978 midges and water fleas declined in occurrence and horseflies (Tabanidae) became important. The most diverse community of invertebrates inhabited mowed plots in 1977 and 1978. There, water fleas, water mites (Hydrachnidae), and mosquitos (Culicidae) occurred frequently in 1977 and 1978. Moreover, predaceous diving beetles (Dytiscidae) were important in 1977 as were soldier flies (Stratomyiidae) and planorbid snails (Planorbidae) in 1978.

Three arbitrary categories were established to illustrate the distribution of invertebrate size classes relative to basin treatments and years (Table 7). Invertebrate taxa were assigned to categories based on their mean biomass per organism and if their frequency of occurrence was ≥ 10 percent. The numbers of taxa in the smallest category (< 1.0 mg) were more similar among basin treatments than in the intermediate (1.0-2.0 mg) and large (> 2.0 mg) categories. Control and rototilled areas contained fewer intermediate and large-sized invertebrate taxa than did mowed plots. The addition of 2 large-sized taxa on mowed plots in 1978 was explained by the increased occurrence of physid (Physidae) and planorbid snails.

Table 6. Estimated mean (95% C.I.) biomass per organism, and percentage occurrence of aquatic invertebrate taxa by basin treatment, 1977-78.

Taxon	Mean biomass/ organism (mg dry weight)	Basin treatment					
		Control (n=50)		Mowed (n=50)		Rototilled (n=50)	
		1977	1978	1977	1978	1977	1978
Cladocera							
Daphnidae	0.06 ± 0.03 ^a	22 ^b	66	90	94	84	18
Conchostraca							
Lynceidae	0.31 ± 0.02		16		20		4
Hydracarina							
Hydrachnidae	0.18 ± 0.08		2	48	64	6	10
Hemiptera							
Corixidae	3.86 ± 1.08	2	6	20	18	2	4
Coleoptera ^c							
Dytiscidae	1.26 ± 0.82		10	46	24	2	2
Diptera ^c							
Chironomidae	0.59 ± 0.31	100	98	20	7	74	38
Culicidae	1.16 ± 0.86			72	62	4	12
Ceratopogonidae	0.12 ± 0.02		2				2
Psychodidae	0.08 ± 0.01						6
Stratiomyidae	2.16 ± 0.61			10	30	4	4
Syrphidae	0.44 ± 0.04					2	
Tabanidae	1.27 ± 0.52				6		30
Gastropoda							
Lymnaeidae	3.47 ± 0.98			6	6		2
Physidae				6	12		
Planorbidae				4	44		

^aMean ± 95% confidence interval.^bUnderscored percentages correspond to frequently occurring ($\geq 10\%$) taxa.^cLarval forms.

Table 7. Number of frequently occurring ($\geq 10\%$) aquatic invertebrate taxa by biomass category and basin treatment, 1977-78.

Biomass category (mg/organism)	Basin treatment					
	Control		Mowed		Rototilled	
	1977	1978	1977	1978	1977	1978
< 1.0	2	3	3	3	2	3
1.0 - 2.0	0	1	2	2	0	2
> 2.0	0	0	2	4	0	0

DISCUSSION

Drought

Dabbling duck pair use of the study area increased dramatically in the first year following habitat manipulations. The magnitude of response, however, was confounded by drought conditions which were geographically widespread in 1977. High pair numbers in 1977 resulted from significantly more pairs of mallards and blue-winged teal. Study area population levels of mallards and blue-winged teal paralleled higher numbers for these species on the Delta Marsh in 1977 as compared to 1976 or 1978 (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), and Jackson (1979).

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) showed that avian abundance and species diversity was highest in several Iowa marshes during the hemi-marsh phase. Increased water levels and muskrat (Ondatra

zibethica) activity, characteristic of this phase, produce an approximate 50:50 interspersions of emergent hydrophytes and open water. The present study empirically showed that dabbling duck breeding pair densities and species diversity were greatest on 50:50 plots which simulated the hemi-marsh configuration. However, what attributes of the hemi-marsh phase might explain the observed responses? The interaction of 2 factors, amount of habitat patchiness and resource levels of aquatic invertebrates, appears to be influential.

The hemi-marsh phase represents a stage in the successional dynamics of a marsh when habitat patchiness is high due to maximal interspersions of emergent vegetation and open water. Deviations from 50:50 cause a reduction in one of the structural components. It has been well documented that bird species diversity is correlated with increased habitat structural complexity (e.g., Karr and Roth 1971, MacArthur and MacArthur 1961, Recher 1969, Roth 1976, Willson 1974). 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 the present study and others (Möller 1975, Weller and Spatcher 1965, Weller and Fredrickson 1974) strongly suggest that breeding dabbling duck abundance and species diversity is influenced in part by the amount of habitat patchiness.

Another factor apparently linked to the structural and functional aspects of the hemi-marsh is high population levels of aquatic invertebrates. Voigts (1976) and Whitman (1974, 1976) recorded high numbers as well as 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 3-5 year old beaver ponds which contained plentiful amounts of emergents. Large quantities of emergent litter are annually broken down during the hemi-marsh phase by fragmentation, toppling, and muskrats (Davis and van der Valk 1978) providing a detrital substrate that sustains high invertebrate populations. The vital role of aquatic invertebrates, as a source of protein and essential amino acids for egg-laying hens, has been documented (Swanson et al. 1979). Thus, abundance and diversity of breeding dabbling ducks appear to be influenced by an interaction of habitat patchiness and its indirect effects on resource levels of aquatic invertebrates. Perhaps breeding dabblers as well as other marsh birds use vegetation-water interspersion as a proximate cue (Hilden 1965) to guide themselves into habitats rich in aquatic invertebrates.

An alternative and more simplistic hypothesis would be that the high dabbler abundance and diversity on 50:50 plots was merely a correlate of more available water area and/or openings per plot. If this was true, a greater response to plots with 30 percent vegetation and 70 percent water should have occurred unless social constraints precluded a more complete use of these. In 1978, social interactions among conspecifics at least did not seemingly 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 density of dabbler pairs on 30:70 and 70:30 plots might represent pairs that invaded or were displaced from 50:50 plots. Fretwell and Lucas (1969) theorized that, as population density

increases on preferred habitats, density dependent effects render sub-optimal habitats equally suitable in terms of fitness prospects.

Percentage ratios of emergent vegetation to water did not influence aquatic invertebrate abundance, biomass, or number of taxa in 1977 or 1978. This seems paradoxical considering the consistently greater dabbler pair densities and species diversity on 50:50 plots. Each year the plots were inundated for approximately 2 months after which time the water was drawn down and the study terminated because of regenerating vegetation. Although the density of vegetation was less on rototilled plots, visually there was little structural difference between manipulated and unmanipulated areas by late June each year. Perhaps the plots did not retain their vegetative-water configuration long enough each year to manifest structural and/or functional differences to invertebrate fauna. Wetlands that undergo natural or artificially imposed successional changes exhibit definite phase-related differences in invertebrate population levels (Reinecke 1977, Voigts 1976, Whitman 1974, 1976).

Basin Treatment

With the exception of blue-winged teal and pintails in 1978, basin treatment (mowed or rototilled) did not influence dabbler pair densities. Perhaps the acquisition of 'space' by breeding dabbling ducks had an overriding effect on resource levels of aquatic invertebrates which were affected by basin treatment. The greater pair densities of blue-winged teal and pintails on mowed plots in 1978 were probably related to the abundance of snails (primarily planorbids) on those plots. Breeding blue-winged teal (Dirschl 1969, Swanson et al. 1974) and

pintails (Krapu 1974) forage preferentially on snails when available.

An inconsistent response in dabbling species diversity arose between 1977 and 1978 relative to basin treatments. Although the differences in species diversity between mowed and rototilled plots were not statistically significant, diversity values were slightly higher for rototilled plots in 1977 whereas the opposite was true in 1978. Dabbling pair abundance paralleled species diversity in both years. Since species richness and relative abundance are employed in the calculation of Brillouin's diversity index, the numerical effect of abundance appeared responsible for this result.

Other studies have shown distinct sex-related differences in breeding dabbling activity, particularly in greater female foraging rate (Afton 1979, Derrickson 1977, Dwyer 1975, Dwyer et al. 1979, Seymour and Titman 1978, Stewart and Titman 1979, Titman 1973). In this study there were only slight differences between pair members and single male dabbling ducks based on activity data. My data could not be chronologically partitioned because the reproductive status of individuals was unknown. This seasonal pooling of data undoubtedly magnified among-group variation and masked any real differences.

Significant differences existed between basin treatments in the percentage occurrence of dabbling activities, although the extent of these differences was insufficient to accurately classify basin treatments by the measured activity categories. Clearly, activities unique to basin-treatment types were not apparent. The most dramatic difference with respect to basin treatments for all dabblers in both years was in the percentage occurrence of foraging and locomotor activity. These 2 activities were inversely related, inferring that

when dabblers foraged frequently over a particular basin type less time was expended moving between feeding patches.

The mean percentage of foraging for each dabbler species within basin treatments was correlated with the corresponding mean invertebrate abundance in 1977 ($r = 0.80$, $df = 13$, $P < 0.01$) and 1978 ($r = 0.59$, $df = 13$, $P < 0.05$). An obvious conclusion would be that the frequency of dabbler foraging was directly influenced by encounter rate with potential prey items, and this may serve as a proximate cue for time expenditures within feeding patches as suggested by Royama (1970). However, it is incomplete to interpret foraging strategies on the basis of prey numbers alone. Prey abundance and ingested biomass interact to determine dietary benefits relative to foraging costs (Schoener 1971, Pyke et al. 1977). In 1977, the percentage of foraging for all dabbler species was highest on control areas which also had the greatest mean abundance and biomass of aquatic invertebrates. When the mean biomass estimate for each basin category was divided by its corresponding mean abundance, the net return (in energy and/or nutrition) potentially available to dabblers was over 10 times greater on the control area than on mowed or rototilled plots in 1977. Dabblers seemingly matched their greatest foraging effort in 1977 with the most 'profitable' (Royama 1970) feeding patch. In 1978, the mean percentage occurrence of dabbler foraging was highest on mowed plots. Indicative of mowed plots in 1978 was the lowest mean invertebrate biomass notwithstanding mowed plots' high mean invertebrate abundance. The high abundance of invertebrates on mowed plots was caused by extremely large numbers of water fleas and clam shrimps which contributed little to the estimate of mean biomass. It appeared that the greatest dabbler foraging effort

in 1978 was not matched with the most profitable patch unless mowed plots were unique in some aspect. Further examination of that year's invertebrate data revealed that mowed plots contained the greatest abundance and frequency of occurrence of intermediate and large-sized invertebrate taxa. These larger organisms included water boatmen (Corixidae), predaceous diving beetles, dipterans (mosquitos and soldier flies), and snails. Searching times for these larger organisms might increase due to their lesser abundance in comparison to water fleas and clam shrimps, but total foraging time may be less because fewer larger organisms would have to be ingested to fulfill dietary requirements. Drobney (1977) presented evidence of an inverse relationship between relative invertebrate size and estimated consumption rates necessary to satisfy daily protein needs of breeding female wood ducks (Aix sponsa). The high frequency of foraging on mowed plots in 1978 may reflect a response by dabblers to these larger invertebrates; the abundance of which remained the same (water boatmen, mosquitos, diving beetles) or increased significantly (soldier flies, snails) between years. The credibility of the hypothesis cannot be verified without a knowledge of diet composition. However, studies of dabbler feeding ecology have shown that breeding blue-winged teal (Dirschl 1969, Swanson et al. 1974) and pintails (Krapu 1974) selectively forage on dipterans and snails; gadwalls (Serie and Swanson 1976, Swanson et al. 1979) on dipterans, diving beetles, and to a lesser extent on crustaceans (e.g., water fleas, clam shrimps); and mallards (Perret 1962, Swanson et al. 1979) frequently consume dipterans and snails. Breeding dabblers infrequently consume water boatmen (Swanson et al. 1979) even though this invertebrate is high in energy and protein (Reinecke 1977, Sugden 1969). Water

boatmen are extremely mobile and dabblers may find them difficult to capture. Shovelers specialize on crustaceans, but planorbid snails are also important prey items (Swanson and Nelson 1970, Swanson et al. 1979).

Marshes are dynamic environments and in turn aquatic invertebrate populations fluctuate temporally and spatially (Orians 1973). Consequently, breeding dabblers apparently continue to search patches and forage disproportionately within them in response to changing resource levels of aquatic invertebrates. The high frequency of foraging on control areas in 1977 and subsequently on mowed areas in 1978 supports this contention. In habitats with predictable food resource levels, optimal foraging theory predicts that animals should forage only in patches which consistently yield the highest energetic and/or nutritional return; a strategy unlikely to be adaptive in wetlands with fluctuating prey resources. Instead dabblers appear to gauge their foraging effort by the current profitability of encountered patches. This idea was originally hypothesized for titmice (Paridae) by Royama (1970) and more recently supported with experimental evidence by Smith and Sweatman (1974). Data must be gathered concurrently on invertebrate dispersion patterns, their relative abundance and biomass, dabbler time expenditures within and between patches, and dabbler diet composition to rigorously test this hypothesis.

Basin treatments also had a striking effect on resource levels of aquatic invertebrates. Invertebrate abundance, biomass, and number of taxa differed between control, mowed, and rototilled areas in 1977 and 1978. It is recognized 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, and were effective in capturing benthic as well as nektonic invertebrates. Thus, their relative efficiencies in extracting invertebrates from the environment was assumed to be similar.

The majority of invertebrate taxa, 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 taxa fluctuated as is typical of the dynamic nature of aquatic invertebrate populations (Swanson and Meyer 1977); however, the percentage change in abundance and biomass was least on mowed plots. Furthermore, mowed plots contained the most diverse community of invertebrates as well as a preponderance of large-sized organisms. This concurs with observations of Swanson et al. (1974) for seasonally flooded wetlands which are structurally and functionally similar to mowed plots in this study. Rototilled basins were intermediate and control areas were lowest in invertebrate faunal diversity and numbers of large organisms, probably because their basins were depauperate in detritus. The rich community of invertebrates on mowed basins was attributed to the abundance of decomposing detritus which also provided an additional structural dimension for invertebrate habitation. Energy and nutrients are contained in detritus and microbes anabolize these constituents during decomposition. Colonization of detritus by micro-organisms provides an important food source for aquatic invertebrates (Berrie 1976, Baker and Bradman 1976, Darnell 1964, Keefe 1972, Swanson et al. 1974, Swanson and Meyer 1977) which in turn are exploited by breeding dabbling ducks (Swanson et al. 1979).

Space and Food

Significantly more dabbling pursuit flights arose from 50:50 plots and mowed areas in 1978. A possible explanation for the disproportionate occurrence of pursuit flights from 50:50 plots is that more dabbling pairs were initially attracted to these plots because of their hemi-marsh configuration, and then evicted by a male conspecific that currently defended the area. The confounding effect of habitat structure and the conspecific's presence, as potential attractants, cannot be separated. As previously discussed, mowed plots may have been superior to rototilled plots in 1978 with respect to resource levels of aquatic invertebrates, and the greater establishment of defended areas within mowed plots may reflect this. In territorial Anas species with long-term pair bonds like shovelers (Afton 1979, McKinney 1975, Seymour 1974), blue-winged teal (Stewart and Titman 1979), and gadwalls (Dwyer 1974), male defense of an area apparently secures a food supply for the female as well as providing her with uninterrupted foraging time. This strategy may also be operative, but on a more short-term basis, among other Anas species as suggested for pintails (Derrickson 1977) and black ducks (Seymour and Titman 1978). Thus, territorial site establishment by breeding dabbling ducks is presumably influenced by an interaction of available water area (i.e., space) and food resources. This is an expansion of Patterson's (1976) conclusion that only space 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.

RECOMMENDATIONS

Wetland areas in North America are diminishing at an alarming rate due to competing demands for space from agriculture, industrialization, and urbanization. Preservation, restoration, development and maintenance of wetlands are urgently needed if continental waterfowl populations are not to be jeopardized. Results from this study implicate habitat prescriptions especially appropriate for wetlands that have water-level control. Where these regulatory capabilities are lacking and cannot be provided, the most optimal strategy may simply be wetland preservation.

Interspersion of hydrophytic vegetation and water is one determinant of density and species diversity of breeding dabbling ducks. The response is greatest when 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 wide-spread drought, for example, pair densities could be high due to natural homing and immigration of drought-displaced individuals, but nesting densities and reproductive output might be low (e.g., Mayhew 1955). Waterfowl seemingly exhibit a temporally dynamic reproductive strategy (Nichols et al. 1976), and individuals may withhold reproductive effort in drought years even though suitable habitat conditions may appear to exist on some management areas. Concurrent with habitat manipulations

should be yearly monitoring of target populations (plant and animal) to fully evaluate the impact of manipulations.

Where water-level management is feasible, the most economical and efficient way to produce a hemi-marsh is through drawdowns. Complete dewatering of wetlands in the 'degenerating' or 'lake' marsh phases (van der Valk and Davis 1978) stimulates revegetation of the open basin. With the addition of water results an interspersed vegetation and water. Fragmentation and decomposition, especially of moist-soil plants, proceeds rapidly during this period because of their intolerance to water and lesser fiber content compared to more robust emergents like cattail and bulrush (Godshalk and Wetzel 1978). This input and decomposition of detritus causes invertebrate populations to temporarily flourish. Intervals between drawdowns should not exceed 5 years (Harris and Marshall 1963, Whitman 1974) in order 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 due to dynamic processes (decomposition, soil-water chemical interactions, nutrient cycling, etc.); the interactive effects of which have not been measured. Additional guidelines for effective water-level management have been reviewed elsewhere (Bellrose and Low 1978, Weller 1978).

Mowing in winter, prior to significant snow accumulation, is an expedient means of creating openings in emergents (Weller 1975) as well as accelerating the fragmentation of detritus. Upon subsequent flooding, cattail regeneration will be inhibited if water levels are maintained (Weller 1975). A random or uniform dispersion of openings should be better than clumping openings which might over aggregate

breeding birds. The number of openings necessary to achieve a 50:50 ratio of vegetation and water depends on their size. Size of openings and subsequent responses by marsh birds has not been adequately tested but appears to vary according to species distance requirements for taking flight (Weller 1975). Observations from this 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 strips in a very convoluted manner. This provides more 'edge' than linear strips and reduces visual contacts between conspecific pairs.

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

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 should be undertaken before implementation.

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

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