DABBLING DUCK ACTIVITY AND FORAGING RESPONSES TO AQUATIC MACROINVERTEBRATES

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ABSTRACT.—Pairs and solitary males of five species of dabbling ducks (Mallard, *Anas platyrhynchos*; Blue-winged Teal, *A. discors*; Northern Shoveler, *A. clypeata*; Gadwall, *A. strepera*; Pintail, *A. acuta*) were observed during April and May 1977 and 1978 to study activity patterns of birds that used artificially manipulated and untreated habitats of the Delta Marsh, Manitoba. Concurrently, samples of aquatic macroinvertebrates were collected in both habitats to relate the frequency of dabbler foraging to estimates of available food resources. Habitat treatments included either mowing of existing emergent hydrophytes or basin scarification by rototilling in late summer, followed by flooding the subsequent spring. Foraging and locomotion were most frequently observed and were negatively correlated in both years. Females foraged more than their mates, whereas solitary males fed least among all. Males in consort with their mates exhibited more alert behavior than was expected by chance alone. Foraging by all species occurred most frequently on control areas in 1977 and mowed areas in 1978. Abundance, biomass (dry weight), and composition of aquatic invertebrate communities varied among habitat treatments within and between years. Dabbling ducks seemingly gauge their foraging effort within patches by sampling the current abundance, biomass, and perhaps nutritive quality of potential invertebrate prey. This interpretation conforms with theory and empirical evidence for animals inhabiting environments with unstable food resources. *Received 13 August 1979, accepted 26 July 1980.*

CONSIDERABLE recent attention has been devoted to time-activity budgets of breeding dabbling ducks (Dwyer 1975, Derrickson 1977, Seymour and Titman 1978, Afton 1979, Dwyer et al. 1979, Stewart and Titman 1980). A consistent pattern emerging from these studies is that sexual differences exist in time allocations. Paramount among these is that females forage more than males, especially during prenesting and egg laying. This is apparently a consequence of the greater energetic demands incurred by nesting females (Ricklefs 1974), as well as of males' increased time investment in mate and/or territory defense.

The activity of breeding dabbling ducks has not been studied in relation to artificial manipulations of wetland habitat. As part of an experimental field study of habitat selection by breeding dabbling ducks (Kaminski and Prince in press), we sampled the diurnal activity of five species (Mallard, *Anas platyrhynchos*; Blue-winged Teal, *A. discors*; Northern Shoveler, *A. clypeata*; Gadwall, *A. strepera*; Pintail, *A. acuta*) that used manipulated and untreated habitats of the Delta Marsh, Manitoba during April and May 1977 and 1978. Our first objective was to test the hypothesis that the frequency with which dabbling ducks exhibited six categories of activity would depend on sex-consort status (i.e. pair members in consort or solitary males) and habitat treatment. We also wished to test the hypothesis that habitat treatments would influence resource levels of aquatic macroinvertebrates and that this would be reflected in the frequency of occurrence of dabbler foraging. Aquatic invertebrates dominate in the diets of breeding hens, providing an external source

of essential amino acids for egg production (Swanson et al. 1979). Work by Royama (1970) and Smith and Sweatman (1974) on Great Tit (*Parus major*) foraging behavior in prey-fluctuating environments, coupled with the knowledge that aquatic invertebrate populations are temporally and spatially variable (Weller 1979), led us to predict that dabbling ducks would vary their foraging effort within patches according to the abundance and biomass of potentially available invertebrate prey.

STUDY AREA AND METHODS

Study area.—The study was conducted on the Delta Marsh in southcentral Manitoba (50°11'N, 98°19'W), approximately 2 km east of the Delta Waterfowl Research Station. Study sites included a 33-ha impoundment, where habitat manipulations were performed, and two adjacent bays of the marsh, which served as a control area. In March 1977, an earthen dike was constructed enabling control of water levels within the impoundment.

Originally, an unbroken dense stand of emergent hydrophytes covered the impounded area. Thus, there was no existing natural interspersion of vegetation and open water to confound experimental levels of emergent cover and water. The predominant plant species within the impoundment was whitetop grass (*Scolochloa festucacea*), covering 60% of the area. Other emergents included giant reed (*Phragmites australis*, 30%), cattail (*Typha latifolia*, 5%), and sedge (*Carex* spp., 5%). Shorelines of the two control bays were rimmed with cattail, giant reed, and bulrush (*Scirpus* spp.). Kaminski and Prince (in press) provide a more detailed description of the study area.

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 within the impoundment. Habitat manipulations began in August 1976 when the soil was sufficiently dry to support a tractor.

A diagrammatic example of plot design is illustrated 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 three replicates of six treatment combinations that were randomly assigned to plots. Vegetation was mowed with a tractor-drawn rotary mower within the area of 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. The centers of circles were randomly located from nine possible points per plot to minimize positional bias. Plant litter was left lying where mowing was the specified treatment. 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. Concentric paths were followed while mowing and rototilling to distribute treatment effects evenly. The plot treatments of 1976 were repeated in August 1977 in preparation for the 1978 season. Burning prior to the second rototilling operation in 1977 was not necessary due to reduced plant regeneration.

The impoundment was inundated between 11–19 April 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. Open water appeared in all circles following inundation, and ANOVA revealed no difference ($P > 0.05$) in weekly ($n = 6$ in 1977; 5 in 1978) sampled water depths among five sites randomly located within the impoundment. Water depth was maintained at 32 ± 3 cm until 3–7 June 1977 and 1978, when water levels were completely drawn down. The study was terminated on 30 May 1977 and 1978, because vegetative regrowth biased interspersion levels and complicated observations of ducks.

Behavioral observations.—Unmarked dabbling duck pair members in consort and solitary males, all of unknown reproductive status, were observed on treated and control areas 5 days per week between 19 April and 30 May 1977 and 1978. Concurrent observations were made by two people using 15–60× spotting scopes from elevated blinds. The observers continuously scanned separate sections of the study area during 2-h-long sessions and recorded the current activity of all visible dabblers according to species, sex-consort status (male/female in consort with mate or solitary male), and basin treatment (control, mowed, or rototilled). The procedure was similar to "scan" sampling, which approaches a simultaneous sample of all individuals presently available for observation (Altmann 1974). Activities were broadly categorized as foraging, resting, locomotor, comfort movements, alert, and courtship displays. Starting times for morning and afternoon observation sessions were randomly selected from the hours 0600–1000 and 1300–1500, respectively. Evening sessions began at 1830 or 1900 depending on time of sunset. A total of 292 and 204 man-hours were spent observing in 1977 and 1978, respectively.

LEGEND

EMERGENT HYDROPHYTES

OPEN WATER

% COVER:%WATER

SQUARES 1HA

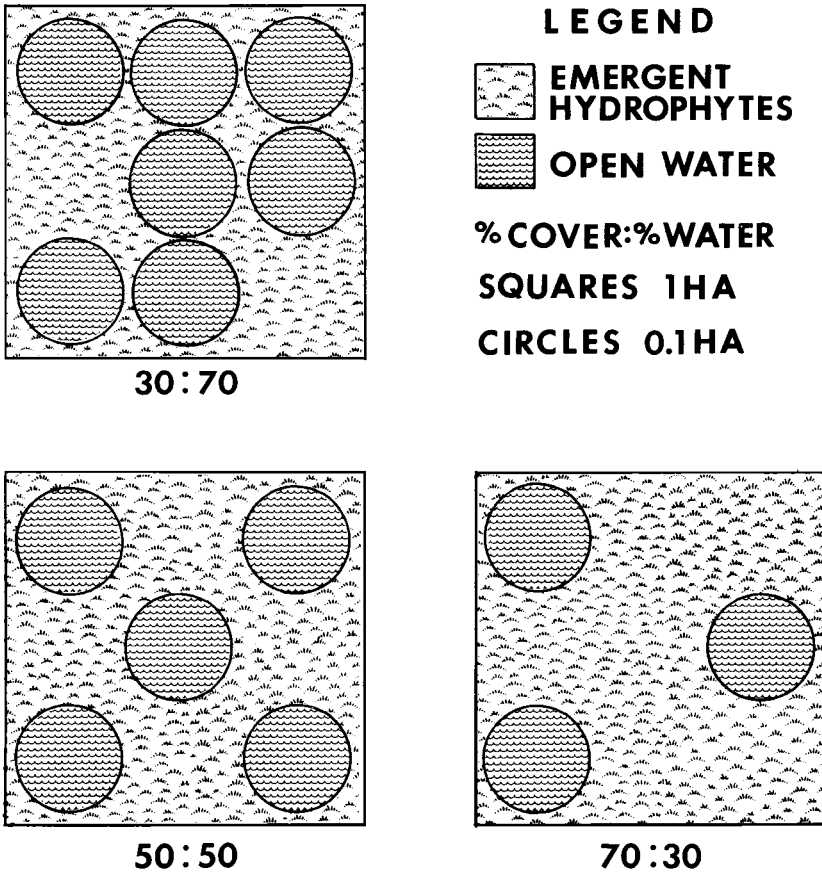CIRCLES 0.1HA

30:70

50:50   70:30

Fig. 1.   A diagrammatic example of experimental plots.

Movements of birds within and between plots precluded censusing birds while making observations. Hence, activity data were not weighted by the estimated number of birds under observation. Statistical analyses of activity data could not be made in a cross-classified manner (i.e. by percentage ratios of vegetation to open water and basin treatments), because the control area lacked fixed levels of vegetation and water and not all plots within the impoundment were visible from the blinds.

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 10 randomly selected mowed and 10 rototilled 0.1-ha circles contained within plots representing each cover-water treatment. Ten randomly located open-water sites within one of the control bays that was similar in depth to the impoundment were also sampled. 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: 22, Fig. 3.11), was used to sample rototilled circles and control sites. The corer did not function on mowed circles because of interference with mowed 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. Both samplers enclosed a volume of water from surface to substrate and were effective in collecting benthos and nekton. Thus, we assumed that the samplers functioned similarly in extracting invertebrates from the environment. 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 l water), which floated invertebrates to the surface for ease of sorting (Flannagan 1973). Invertebrates were identified to family using Merritt and Cummins (1978) and Pennak (1953) and counted, and a sample of each family was oven dried (105°C) for 24 h (Cummins and Wuycheck 1971) and then weighed on a Mettler H-54 balance.

TABLE 1. Percentage occurrence of activities for five dabbling duck species in 1977 and 1978.[a]

| Species | Year | Activity | | | | | | Number of observations |
		Forage	Loco-motor	Com-fort	Rest	Alert	Court-ship	
Mallard	1977	60.7	14.3	9.6	10.8	4.3	0.3	4,160
	1978	42.0	32.3	11.1	7.9	5.9	0.8	1,250
Blue-winged Teal	1977	65.7	15.8	8.1	6.5	1.1	2.8	6,989
	1978	42.7	34.1	10.9	4.7	2.6	5.0	2,589
Shoveler	1977	51.3	18.5	13.4	9.1	2.4	5.3	1,823
	1978	39.6	31.1	16.7	6.4	2.7	3.5	841
Gadwall	1977	54.8	22.6	13.1	4.8	3.2	1.5	890
	1978	39.6	33.3	11.4	9.8	4.7	1.2	1,278
Pintail	1977	72.8	8.2	8.2	1.4	9.5	0.4	851
	1978	37.1	31.0	8.3	10.1	12.1	1.4	586

[a] Frequencies were weighted during computation of percentages to adjust for unequal numbers of observations of activity between combinations of sex-consort status and basin treatment.

RESULTS

Dabbler activity.—Dabbling ducks engaged most frequently in foraging activity in 1977 and 1978 (Table 1). Among the five species, foraging accounted for 51–73% ($\bar{x}$ = 61%) and 37–43% ($\bar{x}$ = 40%) of all activities in 1977 and 1978, respectively. Locomotor activity ranked second in order of occurrence, ranging among species from 8 to 23% ($\bar{x}$ = 16%) in 1977 and 31 to 34% ($\bar{x}$ = 32%) in 1978. Largely because foraging and locomotion were the predominant activities in both years, their frequencies of occurrence were negatively correlated in 1977 (r = −0.71, df = 43, $P <$ 0.01) and 1978 (r = −0.78, df = 43, $P <$ 0.01) over all dabbling duck species, basin treatments, and sex-consort statuses. There was a marked decrease in foraging activity between 1977 and 1978, and, consequently, an increase in locomotion was recorded in 1978. The occurrence of comfort movements generally exceeded resting activity within species and years. Except for notable amounts of alert activity by

TABLE 2. Results of *G*-tests of independence and interaction among activity (A), basin treatment (BT), and sex-consort status (SCS).

| Species | Year | Independence | | | Interaction |
		A-BT-SCS (44)[a]	A-BT (10)	A-SCS (10)	A × BT × SCS (20)
Mallard	1977	*G* = 966**[b]	480**	78**	106**
	1978	313**	163**	110**	30 NS
Blue-winged Teal	1977	1,157**	848**	147**	56**
	1978	429**	259**	95**	49**
Shoveler	1977	491**	159**	112**	9 NS
	1978	192**	112**	34**	24 NS
Gadwall	1977	155**	91**	39**	20 NS
	1978	284**	140**	85**	48**
Pintail	1977	198**	124**	40**	21 NS
	1978	170**	63**	31**	37*

[a] Degrees of freedom for χ^2 critical value.
[b] * = ($P <$ 0.05), ** = ($P <$ 0.005), NS = ($P >$ 0.05).

TABLE 3.   Percentage occurrence of foraging by dabbling duck pair members in consort with their mates and by solitary males in 1977 and 1978.[a]

Species	Year	Pair members in consort		Solitary male
		Female	Male	
Mallard	1977	66.5 (1,246)[b]	58.8 (1,244)	56.9 (1,670)
	1978	53.8 (413)	42.1 (416)	30.0 (421)
Blue-winged Teal	1977	69.8 (2,171)	68.1 (2,128)	59.2 (2,690)
	1978	58.8 (603)	46.2 (599)	33.5 (1,387)
Shoveler	1977	56.7 (603)	53.8 (614)	43.4 (606)
	1978	59.5 (196)	42.0 (199)	30.5 (446)
Gadwall	1977	61.6 (399)	55.9 (400)	46.7 (91)
	1978	52.3 (544)	43.3 (555)	23.1 (179)
Pintail	1977	75.2 (301)	70.7 (309)	71.3 (241)
	1978	46.1 (200)	31.7 (201)	33.5 (185)

[a] Frequencies were weighted during computation of percentages to adjust for unequal numbers of observations of foraging between basin treatments.
[b] Number of observations of all activities.

Pintails in 1977 (10%) and 1978 (12%), alert and courtship behaviors comprised relatively minor proportions of the ducks' behavioral repertoire during each year.

We tested for independence and interaction among categories of activity, basin treatment, and sex-consort status using multiway contingency table *G*-tests (Sokal and Rohlf 1969: 601). Clearly, the frequency of occurrence of activities was not jointly independent of basin treatment and sex-consort status (Table 2). This suggested that additional *G*-tests were required to elucidate the nature of this lack of independence. Activity data from both years and for all dabbler species showed a strong dependence on sex-consort status and basin treatment. Basin treatment, however, had more influence on the occurrence of activities than did sex-consort status, as evidenced by the higher values of the *G*-test statistics for the former criterion. Although dabbler activity was dependent on basin treatment and sex consort status, the *G*-test statistics are probably inflated somewhat, because foraging and locomotion were correlated, causing the observed frequencies to depart from expected values.

Unlike the *G*-tests of independence among activity, sex-consort status, and basin treatment, tests for interaction among the three criteria did not expose a regular pattern of significance (Table 2). There was interaction among the factors in 1977 and 1978 only for Blue-winged Teal and no interaction in either year for Shovelers. Mallards, Gadwalls, and Pintails showed interaction in one of the years.

A graded series was apparent with respect to the frequency of dabbler foraging relative to sex-consort status in 1977 and 1978 (Table 3). Female dabbling ducks (of all species) accompanied by their mates foraged more than their mates, and solitary males (except Pintails) fed least among all. This pattern was reversed for locomotor activity, owing to the inverse relationship between foraging and locomotion. Moreover, when pair members consorted, males and females engaged in less locomotion, whereas solitary males exhibited more locomotion than was expected by chance alone. Females exhibited the least amount of alert behavior (i.e. always less than the calculated expected values). In contrast, males accompanying their females were alert most frequently (expected values were always less than observed frequencies).

Foraging by all dabbler species was most frequently observed on the control area

TABLE 4. Percentage occurrence of foraging arrayed by basin treatment within dabbling duck species and years.[a]

Species	Year	Basin treatment		
		Control	Mowed	Rototilled
Mallard	1977	79.2 (1,367)[b]	54.8 (1,434)	48.2 (1,359)
	1978	35.5 (423)	61.7 (491)	28.6 (336)
Blue-winged Teal	1977	86.8 (1,730)	61.0 (1,966)	49.2 (3,293)
	1978	44.1 (96)	58.6 (1,322)	25.4 (1,171)
Shoveler	1977	65.2 (273)	36.6 (268)	52.1 (1,282)
	1978	24.5 (62)	59.8 (523)	34.6 (256)
Gadwall	1977	62.6 (442)	61.8 (104)	39.8 (344)
	1978	29.2 (603)	48.8 (264)	40.7 (411)
Pintail	1977	89.3 (154)	69.5 (433)	58.3 (264)
	1978	45.8 (112)	55.1 (418)	10.3 (56)

[a] Frequencies were weighted during computation of percentages to adjust for unequal numbers of observations of foraging between sex-consort statuses.
[b] Number of observations of all activities.

in 1977, whereas its greatest occurrence in 1978 was over mowed areas (Table 4). Although sex-consort status had a significant effect on dabbling duck activity, the data are presented combined at the level of dabbler species, because the greatest occurrence of foraging by consorting pair members and solitary males of all species was recorded for the same basin treatment within years.

Aquatic macroinvertebrates.—Resource levels of aquatic macroinvertebrates varied more in response to basin treatments (control, mowed, and rototilled) than to percentage ratios (30:70, 50:50, and 70:30) of emergent hydrophytes and open water. For samples taken from the impoundment, ANOVA revealed no differences ($P >$ 0.05) in mean invertebrate abundance and biomass (dry weight) due to percentage ratios of vegetation and water in 1977 and 1978. In addition, no interaction ($P >$ 0.05) between percentage ratios of vegetation to water and basin treatments was detected for either year. Invertebrate abundance and biomass were significantly influenced by basin treatments within and between years (Table 5). Mean invertebrate abundance was higher on the control area than on manipulated areas in 1977. In 1978, mean abundance was greatest on mowed areas, intermediate on the control, and lowest on rototilled plots. Invertebrate numbers decreased on all areas between

TABLE 5. Statistics ($\bar{x}$ and 95% CL)[a] of parameters used to assess resource levels of aquatic invertebrates relative to basin treatments in 1977 and 1978.

Parameter	Year	Basin treatment		
		Control ($n = 50$)	Mowed ($n = 50$)	Rototilled ($n = 50$)
Organisms/m³	1977	18,906[b] (17,233–20,690)	11,366[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)/m³	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)

[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).

TABLE 6. Mean biomass (dry weight) per organism and percentage occurrence of aquatic invertebrate taxa relative to basin treatments in 1977 and 1978.

	Mean biomass/ organism (mg dry weight)	Basin treatment					
		Control (n = 50)		Mowed (n = 50)		Rototilled (n = 50)	
Taxon		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
Stratomyiidae	2.16 ± 0.61			*10*	*30*	4	
Syrphidae	0.44 ± 0.04					2	4
Tabanidae	1.27 ± 0.52				6		*30*
Gastropoda	3.47 ± 0.98						
Lymnaeidae				6	6		
Physidae				6	*12*		2
Planorbidae				4	*44*		

[a] Mean ± 95% CI.
[b] Italicized percentages correspond to frequently occurring (≥10%) taxa.
[c] Larval forms.

1977 and 1978. The decline was least dramatic on mowed (27%, $P > 0.05$), however, in comparison to control (63%, $P < 0.05$) or rototilled (64%, $P < 0.05$) areas. Although the greatest mean biomass of invertebrates occurred on the control area in 1977 and 1978, biomass estimates for the control decreased ($P < 0.05$) between years and increased ($P < 0.05$) on mowed and rototilled areas. Mean biomass estimates for mowed and rototilled areas were similar in 1977 but were less for mowed than rototilled in 1978.

Variation between years in the percentage occurrence of aquatic invertebrate families within basin treatments and the mean biomass per organism are presented in Table 6. Samples from the control area contained the fewest families in 1977 and 1978, being dominated by midge larvae (Chironomidae) and water fleas (Daphnidae). A similar assemblage 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 greatest number of invertebrate families was found on mowed plots in 1977 and 1978. There, water fleas, water mites (Hydrachnidae), and mosquito larvae (Culicidae) occurred frequently in 1977 and 1978. Additionally, predaceous diving beetle larvae (Dytiscidae) were important in 1977 as were soldier fly larvae (Stratomyiidae) and snails (Planorbidae) in 1978.

Three arbitrary biomass categories were established to illustrate the numerical distribution of invertebrate families relative to basin treatments and years (Table 7).

TABLE 7. Number of frequently occurring (≥10%) invertebrate families relative to biomass category and basin treatment in 1977 and 1978.

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

Invertebrate families were assigned to categories based on their mean biomass per organism if their frequency of occurrence was equal to or greater than 10%. The numbers of families in the small category (<1.0 mg) were most similar among basin treatments. Control and rototilled areas contained fewer intermediate (1.0–2.0 mg) and large-sized (>2.0 mg) invertebrate families than did mowed areas. The addition of two large-sized families on mowed plots in 1978 resulted from the increased occurrence of physid and planorbid snails.

DISCUSSION

Recent time-activity analyses (Dwyer 1975, Derrickson 1977, Seymour and Titman 1978, Afton 1979, Dwyer et al. 1979, Stewart and Titman 1980) have demonstrated marked sexual differences in activity budgets of breeding dabbling ducks. Most striking is the difference in rate of foraging between males and females; females feed more in order to fulfill higher energetic/nutritional demands of reproduction (Ricklefs 1974). Another particularly evident pattern is the exhibition of more alert behavior by males in consort with their mates. Increased alert behavior while the male accompanies his mate affords the female greater undisturbed feeding time, guards against encounters with predators, and lessens potential for harassment and rape by male conspecifics (Derrickson 1977). Results presented here on patterns of foraging and alert behavior for consorting pair members agree with these earlier findings. Unlike the above studies, however, we were unable to partition activity budgets chronologically (e.g. prenesting, egg laying, incubation), because the reproductive status of individuals was unknown.

Solitary males engaged in less feeding and more locomotion than males in the company of their mates. We cannot interpret this finding properly without knowing the pair status of solitary males and the reproductive state of their mates, if these males were paired. R. Wishart (pers. comm.) indicates for American Wigeon (*A. americana*) that paired males in consort with their mates during egg laying and solitary unpaired males exhibit very similar amounts of feeding and locomotion. When laying females are not in the company of their mates, however, paired Wigeon males respond to their absence by feeding less and becoming more mobile through interactions (e.g. territory defense, rape attempts) with conspecifics.

As predicted, aquatic invertebrate resources varied between basin treatments and, in turn, so did the occurrence of dabbler feeding activity. Percentage occurrence of foraging by each dabbler species within basin treatments was directly correlated with the corresponding mean invertebrate abundance in 1977 ($r = 0.76$, df = 13, $P < 0.01$) and 1978 ($r = 0.73$, df = 13, $P < 0.01$). An obvious conclusion might be that dabbler foraging rate was directly influenced by encounter frequency with prey items, and this could serve as a proximate cue for determining time expenditures

within feeding patches, as suggested by Royama (1970). It is incomplete, however, to interpret foraging strategies based on prey numbers alone. Prey abundance and ingested biomass interact to determine dietary benefits relative to foraging costs (Schoener 1971). In 1977, the percentage occurrence of foraging for all dabbler species was highest on control areas, which had the greatest mean abundance and biomass of aquatic invertebrates. When the mean biomass estimate for each basin treatment is divided by its corresponding mean abundance, the gross return (in energy and/or nutrition) potentially available to dabblers was over 10 times greater on the control area than on mowed or rototilled areas in 1977. Thus, dabblers seemed to match their greatest foraging effort in 1977 with the most "profitable" (Royama 1970) feeding patches.

In 1978, the mean percentage occurrence of dabbler foraging was highest on mowed plots. Mowed plots in 1978 had the lowest mean invertebrate biomass, notwithstanding their high mean invertebrate abundance. The high abundance of invertebrates on mowed plots was caused by extremely large numbers of water fleas and clam shrimps (Lynceidae), which contributed little to the estimate of biomass due to their small size. It appeared that the greatest foraging effort by dabblers in 1978 was not matched with the most profitable patches unless mowed plots were unique in some aspect. Further examination of the 1978 data revealed that mowed plots contained the greatest abundance and frequency of occurrence of intermediate and large-sized invertebrate families. These larger organisms included water boatmen (Corixidae), predaceous diving beetles, dipterans (mosquitos and soldier flies), and snails. Searching and handling times for these larger organisms might increase due to their lesser abundance and larger size compared to water fleas and clam shrimps, but total foraging time may be less, because fewer larger organisms would have to be ingested to meet dietary requirements. Drobney (1977) presented evidence implicating 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, whose abundance remained the same (water boatmen, mosquitos, diving beetles) or increased significantly (soldier flies, snails) between years.

The credibility of this hypothesis cannot be evaluated without a knowledge of dabbler diet composition. Literature on dabbler feeding ecology, however, indicates 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) forage on dipterans, diving beetles, and 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 (Sugden 1973, Driver et al. 1974, Reinecke 1980). Water boatmen are extremely mobile, and dabblers perhaps find them difficult to capture. Shovelers specialize on crustaceans, but planorbid snails are also important prey (Swanson and Nelson 1970, Swanson et al. 1979).

Our hypothesis does not exclude the possibility that the foraging responses by dabblers may have been linked to nutrient constraints, as suggested by Pulliam (1975). In 1977, dabblers foraged most frequently on control areas, where midge larvae occurred in all invertebrate samples and were more abundant than in 1978. Midges are extremely rich in nutrients (Sugden 1973), forming important food items

for most breeding female dabbling ducks (Swanson et al. 1979). Frequent foraging by dabblers on mowed areas in 1978 coincided with the highest number of invertebrate families of all sampled areas (Kaminski and Prince in press). The probability of acquiring a balanced diet would probably be greatest on mowed areas in 1978 due to the diverse invertebrate fauna. Also in 1978, snail abundance increased significantly on mowed areas. Snails are major foods of most breeding dabblers except Gadwalls (Swanson et al. 1979), constituting important external sources of calcium and protein for egg production (Krapu 1979). Gadwalls prey quite heavily upon crustaceans, especially clam shrimps in nonsaline wetlands (Swanson et al. 1979), which occurred initially and most abundantly on mowed areas in 1978. Thus, it seems possible that dabbling ducks respond not only to invertebrate abundance and biomass but also to patches containing invertebrates capable of satisfying certain nutritional needs.

Marshes are dynamic environments exhibiting temporal and spatial fluctuations in aquatic invertebrate populations (Orians 1973, Weller 1979). Consequently, breeding dabblers apparently continue to search patches and to expend differential amounts of foraging time within them in response to changing resource levels of aquatic invertebrates. The high frequency of dabbler 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 allocate all foraging time to patches that consistently yield the highest energetic and/or nutritional return, a strategy unlikely to be adaptive (or even possible) in wetlands with unstable prey resources. Instead, dabblers appear to gauge their foraging effort by sampling the current profitability of encountered patches. This was also hypothesized by Royama (1970) as the foraging strategy of Great Tits and supported with experimental evidence by Smith and Sweatman (1974).

Pyke et al. (1977) and Krebs (1978) have correctly pointed to the need for more theoretical and experimental work to determine whether or not animals faced with fluctuating prey resources forage optimally as a result of sampling available food resources. Data must be collected concurrently on invertebrate abundance, biomass, nutrient quality, and dispersion pattern, as well as on dabbler diet composition and time expenditures within and between feeding patches to test the optimality hypothesis for *Anas* species rigorously.

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The **Frank M. Chapman Memorial Fund** of the American Museum of Natural History is administered by a committee that meets twice annually to review applications for grants and fellowships. While there is no restriction on who may apply, the Committee particularly welcomes applications from graduate students; management projects and projects by senior investigators are seldom funded. Applications should be submitted not later than **15 February** and **15 September.** Application forms may be obtained from the **Frank M. Chapman Memorial Fund Committee, The American Museum of Natural History, Central Park West at 79th St., New York, NY 10024.**

Dr. Timothy Crowe was appointed a Chapman Fellow for the period April 1981 through March 1982. He will study the systematics, biogeography and adaptive morphology of African gamebirds, hornbills, and diurnal birds of prey.

Dr. Philip Gaddis, also appointed a Chapman Fellow for April 1981 through March 1982, will study vocal communication systems and social behavior of the Plain and Bridled Titmice in the Chiricahua Mountains, Arizona.

Chapman grants during 1980, totalling $41,913 with a mean of $451, were awarded to: John P. Badgerow, use of the vee formation by Canada Geese (*Branta canadensis*) for aerodynamic advantage; Kenneth N. Baker, variation in breeding bird abundances among three state forests within the Connecticut River valley; William H. Baltosser, ecological relationships among nesting hummingbirds; Peter W. Bergstrom, incubation behavior in Wilson's Plover (*Charadrius wilsonius*); Verner P. Bingman, earth's magnetism and the ontogeny of migratory orientation; K. D. Bishop, study of Papua New Guinean *Megapodius* species and study of the West New Britain bird collections; Richard Blacquiere, age-related plumage dimorphism in male American Redstarts (*Setophaga ruticilla*); Kathleen A. Blanchard-French, social behavior of the Atlantic Puffin, *Fratercula arctica*; Peter J. Blancher, food supply and foraging behavior of Cassin's and Western kingbirds; Mary L. Bomberger, aspects of the breeding biology of the Wilson's Phalarope in western Nebraska; Michael James Braun, protein differentiation of hybridizing and reproductively isolated populations of Mexican Red-eyed Towhees; Jeffrey T. Burns, mate-switching in House Wrens; Gregory S. Butcher, coloration in orioles, genus *Icterus*; Michael D. Carter, social organization and parasitic habits of the Bronzed Cowbird (*Molothrus aeneus*); Scott L. Collins, habitat structure and habitat relationships of the Parulidae in Minnesota and Maine; Kevin J. Cook, ecology of the Flammulated Owl in Colorado; Malcolm C. Coulter, 1) importance of behavior to breeding success in terns, and 2) parental investment in breeding according to sex in Common Terns, *Sterna hirundo*; James Allan Cox, chromosomal morphology of the Red-winged Blackbird; Janice R. Crook, song variation and species discrimination in Blue-winged Warblers; James R. Cunningham, breeding biology, vocalization and social behavior of the New Zealand Brown Creeper (*Finschia novaesselandiae*); Robert Lawrence Curry, helping, behavior, breeding-group dynamics, and reproductive success in communal Galápagos mockingbirds; Carlos A. Delannoy, ecology and breeding biology of the Puerto Rican Sharp-shinned Hawk; Robert W. Dickerman, 1) avifauna of the southern Pacific lowlands of Guatemala, and 2) review of the Great Blue Heron, *Ardea herodias*; Bruce B. Edinger, behavioral isolating mechanisms in *Icterus galbula galbula* and *I. g. bullockii* in a zone of sympatry; Bonita Eliason, polygyny in the Blackpoll Warbler; Keith William Emmerson, bird community of the Laurel Forest of Tenerife (Canary