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Postbreeding Ecology of Adult
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POSTBREEDING ECOLOGY OF ADULT MALE MALLARDS

ON THE DELTA MARSH, MANITOBA

By

David Harold Gordon

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ABSTRACT

POSTBREEDING ECOLOGY OF ADULT MALE MALLARDS
ON THE DELTA MARSH, MANITOBA

By

David Harold Gordon

The postbreeding ecology of adult male mallards (*Anas platyrhynchos*) was studied on the Delta Marsh, Manitoba during the summers of 1981-1983. The objective of the study was to determine the environmental requisites of postbreeding male mallards. Specific aspects investigated were habitat utilization, feeding ecology, and behavior.

Home ranges or utilization areas of postbreeding male mallards were considerably smaller than those reported for breeding males. Utilization area size decreased to a minimum during the flightless period, and then increased again as males regained flight capability.

Major habitat components important to postbreeding male mallards using the Delta Marsh were loafing sites, dense flooded emergent vegetation, and shallow open water areas having dense beds of submersed vegetation. Early preflightless and late postflightless males used exposed mudflats or beaches of wave-washed plant fragments along the south edge of large open bays in the marsh for loafing sites. Emergent vegetation was used infrequently. Late preflightless, flightless, and early postflightless males used flooded emergent vegetation extensively. Emergent vegetation provided concealment as well as loafing sites in the form of accumulated fallen vegetation. Emergent vegetation species of importance were hardstem bulrush (*Scirpus acutus*) and cattail

(*Typha* spp.). Shallow aquatic bed areas were used by male mallards as feeding sites throughout the postbreeding period.

The diets of postbreeding male mallards were dominated by plant matter. Only preflightless males consumed a significant amount of animal matter. Sago pondweed (*Potamogeton pectinatus*) foliage and seeds, and hardstem bulrush seeds were important food items for flightless males. Plant foliage and seeds from sago or horned pondweed (*Zanichellia palustris*) were major food items for postflightless males. Food use for postbreeding males in general was related to foods available at feeding sites, rather than specific items that were sought.

Time-activity budgets of postbreeding male mallards were dominated by feeding, resting, and comfort movements, respectively. Postbreeding males spent more time involved in comfort movements and feeding, and less time resting and alert than breeding males. The observed changes in activities as male mallards made the transition from breeding to postbreeding were related to changing behavioral and physiological events.

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INTRODUCTION

INTRODUCTION

For more than 40 years, studies on North American waterfowl have focused on the breeding phase of the annual life cycle (Fredrickson and Drobney 1979). Few studies have considered the nonbreeding period (Reinecke 1981), and most of these have concentrated on migrating and wintering waterfowl. The postbreeding period, defined herein as the interval between involvement in reproductive activities and fall migration, has received little attention from waterfowl biologists. Consequently, a deficiency in our knowledge of waterfowl ecology during the nonbreeding period continues to exist. This study was initiated in response to the absence of adequate information for postbreeding waterfowl.

Fredrickson and Drobney (1979) recommended that studies of waterfowl postbreeding ecology should be designed to provide an understanding of habitat use and resource allocation in relation to the requirements of the organism. The purpose of this study was to determine the environmental requirements of postbreeding mallards using the Delta Marsh. Specific aspects studied were habitat utilization, feeding ecology, and behavior. During all years of the study, efforts were made to acquire data for both male and female mallards. However, due to low numbers of female mallards present on the Delta Marsh throughout the study and various logistical difficulties, collection of data for females was generally unsuccessful. Consequently, the results presented here pertain to adult male mallards only.

Chapter I is devoted to spatial and habitat use of male mallards. Important wetland habitat components are identified and characterized.

Chapter II focuses on diet of male mallards during the postbreeding season. Use of various food items is discussed in relation to their availability in the environment.

Activities of postbreeding male mallards are discussed in Chapter III. Comparisons of daily activity budgets between breeding and postbreeding males are made and explanations are offered.

In Chapter IV, habitat use strategies of postbreeding male mallards are presented. Several hypotheses concerning postbreeding dispersal in relation to wetland habitats used are reviewed in light of the results of this study.

CHAPTER I

HABITAT USE BY POSTBREEDING ADULT MALE MALLARDS ON THE DELTA MARSH, MANITOBA

INTRODUCTION

Postbreeding populations of the Tribe Anatini are characterized by a progressive segregation of individuals from the breeding segment. Adult males congregate on traditionally used wetlands to undergo a prebasic molt, a simultaneous remige molt resulting in a flightless period, and a prealternate molt (Young and Boag 1981). Females involved in incubation and broodrearing remain near the breeding site (Hochbaum 1944, 1955, Salomonsen 1968, Gilmer et al. 1977). Females that are reproductively successful eventually desert their broods, as the young become older, to molt on wetlands usually within or in close proximity to the wetland complex used for broodrearing (Oring 1964, Salomonsen 1968, Gilmer et al. 1977).

Hochbaum (1955) proposed that postbreeding birds may have special ecological requirements. Certainly, the 3 to 4 week period of flightlessness imposes some constraints not experienced during other phases of the annual cycle. Gilmer et al. (1977) proposed that wetlands used by breeding waterfowl may be unsuitable for molting, and conversely, molting areas may be unsuitable for breeding. Wetlands used by molting dabbling ducks are characterized as large freshwater marshes providing permanent shallow water, dense cover, abundant food resources, and seclusion (Hochbaum 1944, Salomonsen 1968, Gilmer et al. 1977). Although general descriptions of postbreeding habitat and use by waterfowl exist in the literature, little effort has been devoted to quantitative studies of this aspect of the waterfowl annual life cycle.

The purpose of this aspect of the study was to document habitat use patterns of postbreeding adult male mallards (*Anas platyrhynchos*). Specifically, habitat use patterns for preflightless, flightless, and postflightless males were examined. The mallard was selected because it is a key representative of the genus *Anas* and to take advantage of the large data base concerning other phases of the annual life cycle available for this species.

STUDY AREA

This study was conducted on the 180-km^2 Delta Marsh (Fig. 1) located along the south shore of Lake Manitoba in southcentral Manitoba (50° 11'N, 98° 19'W). The marsh is characterized by dense stands of *Phragmites*, *Typha*, and *Scirpus* separating interconnecting large and small open water areas (Hochbaum 1944). Field activities were restricted to the East Marsh Unit between the villages of St. Ambrose and Delta. Descriptions of emergent vegetation are provided by Love and Love (1954), Walker (1959, 1965), and MacKenzie (1982). Submerged vegetation communities are described by Anderson and Jones (1976). The physiography of the marsh is described by Elson (1967) and Fenton (1978).

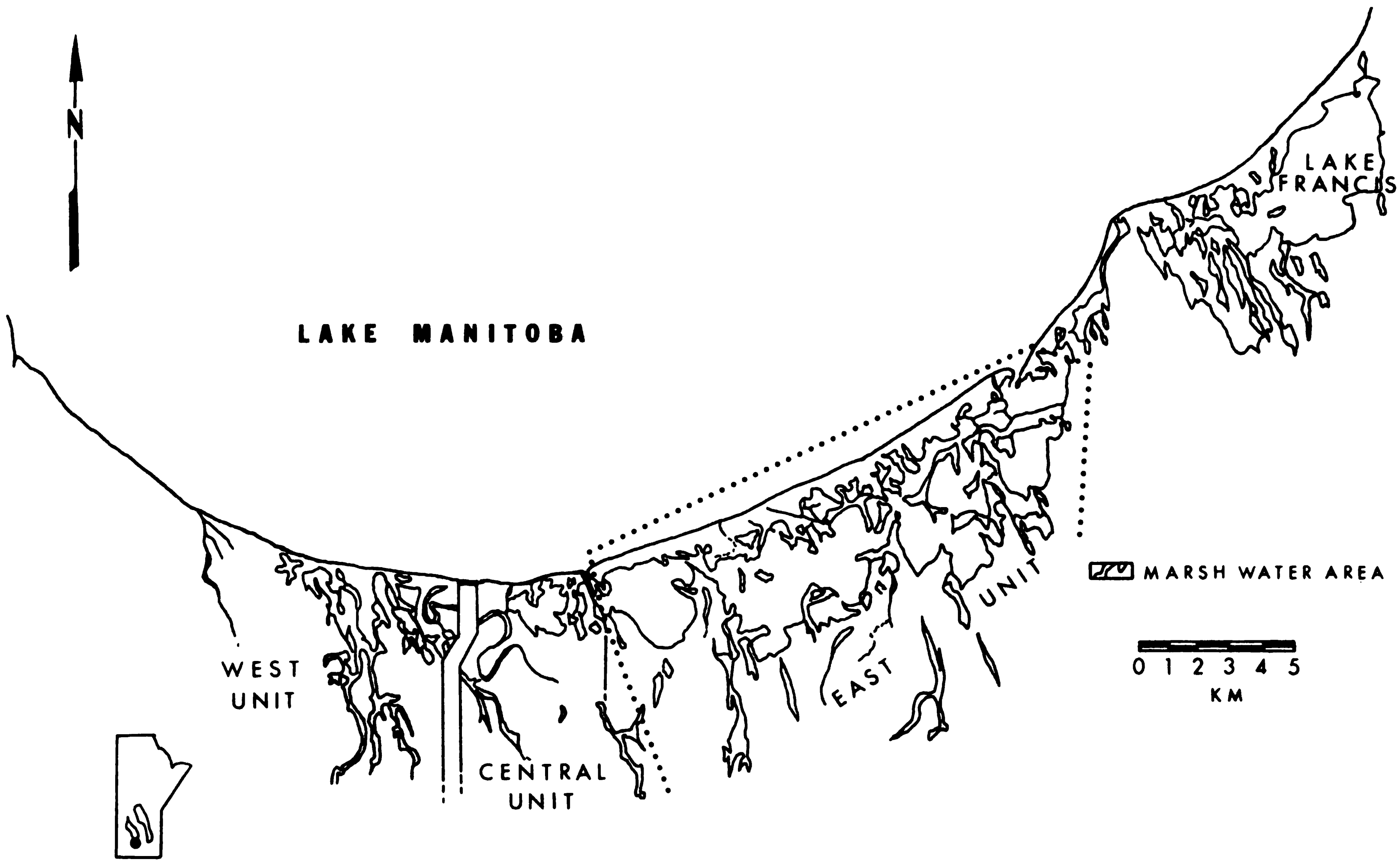

Fig. 1. Delta Marsh. Adapted from Anderson and Jones (1976).

METHODS

Population Counts

Chronology of use of the marsh by adult male mallards was indexed by counts of birds on a 15 ha portion of Portage Creek, a traditional concentration area for postbreeding dabbling ducks on the Delta Marsh. During the summer of 1981 and 1983, weekly mid-day counts were made of the total number of mallards observed on a defined observation area of Portage Creek.

Habitat Use

Habitat use by adult male mallards was evaluated using radio telemetry. Preflightless males were captured using decoy traps (Anderson et al. 1980). Flightless males were captured at night with a dip net from an airboat equipped with spotlights. All males were fitted with colored urethane nasal saddles (Greenwood 1977) bearing an alpha-numeric code, a U. S. Fish and Wildlife Service aluminum leg band, and a backpack radio transmitter similar to one described by Dwyer (1972). Transmitter signals were monitored using 3 fixed-point null-peak antennas mounted on 18 m towers located approximately 2 km apart. Maximum receiving range from the fixed-point antennas varied from 2.5 to 3.0 km. Tests with transmitters placed at known locations revealed location error was $\pm$ 1°. Efforts were made to locate each male 3 times daily. Sampling times within each diurnal period were randomly selected using a random numbers table. Locations of males were determined by triangulation (Mech 1983), plotting azimuths taken simultaneously from 2 towers on large scale base maps delineating major marsh cover types. The 3 major cover types defined were cattail (Typha), bulrush (Scirpus), and aquatic bed (open water with submergent vegetation). Utilization areas were plotted using the minimum convex polygon method (Southwood 1966). The term utilization area is used rather than home-range or activity center to avoid the different interpretations associated with each of these terms.

Radio telemetry data were supplemented with visual observations of preflightless and postflightless males on the Portage Creek concentration area. Observations were made during 2-hour sampling periods randomly selected during diurnal hours (0500-2000 h) using a modified scan-sampling technique (Altman 1974). A defined observation area was scanned continuously throughout each sampling period using a 15-60x spotting scope. Each individual mallard sighted was a sample unit for which the cover type occupied was recorded.

Habitat Measurements

Three replicate measurements of water depth (cm), vertical vegetation density (% cover/m²), horizontal vegetation density (Nudds 1977), and stem density (number/m²) were recorded at randomly selected sample points within each cover type. Sample point locations were selected using radio-locations of mallards within each cover type in order to characterize cover types used. Water depth was measured using an aluminum meter stick. Vertical vegetation density was measured by estimating the percent cover for each species within a 1 m^2 frame. Horizontal vegetation density was quantified by estimating the percent cover for each species at 1/4-meter intervals on a vegetation profile board.

Interspersion of dominant emergent plant communities and aquatic bed areas within habitats used by male mallards was indexed by counting the number of patches of each cover type intercepted by 2 lines drawn across each utilization area. One line was drawn along the longest axis of each utilization area and the second line drawn perpendicular to the first at its midpoint.

Data Analysis

Comparisons of cover type use between preflightless, flightless, and postflightless groups were made using chi-square analysis (Siegel 1956). Cover type use was measured as the percentage of radio locations recorded in each cover type and the percent occurrence of the total individual mallards observed (visual observations of Portage Creek) within each cover type. Differences in utilization area means were compared using a t-test designed for use with small samples having unequal variances and coefficients of variation (Gill 1978:66). Cover type preferences were evaluated for radio-marked mallards using the ranking procedure of Johnson (1980) to compare cover type use and availability. Availability of each cover type was the percent area within each male's utilization area.

Differences in the average number of cover type patches occurring within utilization areas of preflightless, flightless, and postflightless groups were tested using the Median Test (Conover 1971:167). The Kruskal-Wallis Test (Conover 1971:256) was used to test for differences in average cover type patch length among groups.

RESULTS

Movement of postbreeding males into the marsh in mid-June was first apparent with the occurrance of groups of males on traditional concentration areas usually centered around a loafing site near the edge of the marsh (Fig. 2). As birds began the prebasic molt and neared flightlessness, they moved from these concentration areas to sites with flooded emergent vegetation within the marsh interior. The number of mallards on Portage Creek increased until mid-July, followed by a decline in numbers to a low point in late July which coincided with peak numbers of flightless male mallards in the marsh (Fig. 2). As males regained the ability to fly, they eventually centered their activities around these concentration areas again as evidenced by increased numbers of mallards on Portage Creek in August.

Preflightless males observed on the Portage Creek concentration area used aquatic bed areas most frequently (Table 1). Loafing sites in the form of exposed mudflats also received high use. Emergent cover was used infrequently (1%). Although mallards occupying emergent cover were difficult to observe, movements of individuals in and out of emergent stands of vegetation were rare lending confidence to the 1% estimate.

As male mallards moved away from concentration areas with the approach of the flightless period, monitoring habitat use using radio-marked birds was possible as daily movements became restricted.

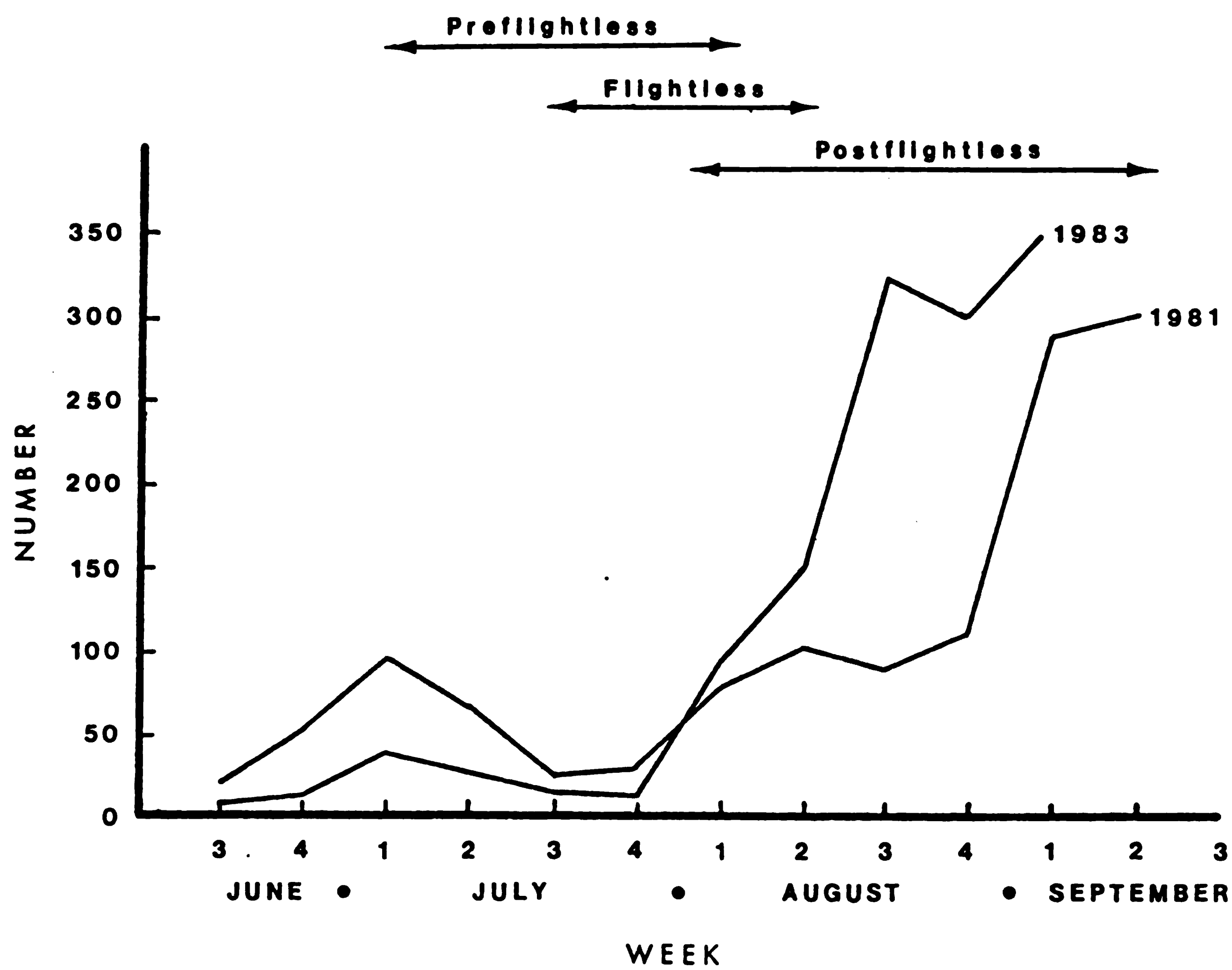

Fig. 2. Total number of mallards observed on the Portage Creek concentration area during weekly mid-day counts. Radio-tracking time periods for preflightless, flightless, and postflightless male mallards are indicated by arrows.

Table 1. Comparison of diurnal cover type use for adult male mallards observed on the Portage Creek concentration area, Delta Marsh, Manitoba. Use is expressed as the percent occurrence of total individuals observed for each cover type.

Cover Type	Preflightless (n = 10328)	Postflightless (n = 5564)
Aquatic Bed	57%	59%
Mudflat	41	40
Emergent	1	1

Three preflightless males were monitored for an average of 17 $\pm$ 10 (sd) days with an average of 63 $\pm$ 52 radio-locations per bird. Ten flightless males were monitored for an average of 13 $\pm$ 6 days and an average of 40 $\pm$ 19 radio-locations were obtained for each bird. Seven postflightless males were monitored for an average of 20 $\pm$ 7 days with an average of 30 $\pm$ 12 radio-locations per bird.

Utilization areas decreased from 21 ha to 6 ha ($P<0.025$, df=2, t=4.942) as male mallards became flightless, and then increased to 43 ha ($p<0.025$, df=6, t=2.691) as males acquired flight capabilities again (Table 2). Diurnal cover type use (Table 3) differed for preflightless and flightless males (x^2 = 37.9, df=1, $p<0.001$), preflightless and postflightless males (x^2 = 6, df=1, $p<0.02$), and flightless and postflightless males (x^2 = 11.8, df=1, $p<0.001$). Preflightless and postflightless males used aquatic bed areas in greater proportion than flightless males.

Use of cover types did not differ from availability for flightless males (F = 0.6763, $p<0.25$) and postflightless males (F = 0.1765, $p<0.50$). Sample sizes for preflightless males were too small to subject to statistical analysis, however, given the observed use and availability for this group (Table 3) it is likely that use of cover types was also proportional to availability.

Nocturnal cover type use was obtained for 5 flightless males (Table 4). The number of nocturnal radio-locations for preflightless and postflightless males were insufficient for meaningful analysis. Nocturnal use of aquatic bed areas was greater than diurnal use for flightless male mallards (x = 28.65, df=1, $p<0.005$).

Table 2. Size (ha) of utilization areas for radio-marked adult male mallards using the Delta Marsh, Manitoba during summer 1981-1983.

Flight Category	N	$\bar{x}$	SE	Range
Preflightless	3	21[a]	1.4	18-23
Flightless	10	6	1.1	1-10
Postflightless	7	43[a]	14.0	10-105

[a]Means significantly different ($p < 0.025$) from flightless category mean for preflightless birds ($t = 4.942$, $df = 2$) and postflightless birds ($t = 2.691$, $df = 6$).

Table 3. Diurnal cover type use (U) and availability (A) for radio-marked adult male mallards using the Delta Marsh, Manitoba. Use is expressed as the percent occurrence of radio-locations within each cover type. Availability is expressed as the percent of the total area (ha) within utilization areas for each cover type.

Cover Type	Preflightless (n = 188)		Flightless (n = 310)		Postflightless (n = 208)	
	U	A	U	A	U	A
Aquatic Bed	62	62	34	46	49	65
Emergent	38	38	66	54	51	35
Bulrush	21	14	29	23	17	9
Cattail	17	24	37	31	34	26

Table 4. Comparison of diurnal and nocturnal cover type use by flightless adult male mallards (n = 5). Use expressed as the percent occurrence of radio-locations within each cover type.

Cover Type	Diurnal Use (n = 17)	Nocturnal Use (n = 49)
Aquatic Bed	19	59
Emergent	81	41

Diurnal cover type use for postflightless male mallards using the Portage Creek concentration area was similar to use by preflightless males on the same area (Table 1). Although analysis of the data indicated a statistical difference in habitat use observed between preflightless and postflightless males ($x^2 = 8.3$, df=2, $p<0.05$), the 2% difference is likely not biologically significant.

Four males marked with radio transmsitters while flightless in the marsh interior were subsequently observed in late summer associated with flocks of postflightless males using traditional concentration sites such as Portage Creek. Repeated observations and radio-locations of 2 of these males revealed a shift in habitat use from feeding in aquatic bed areas to feeding with flocks of males making morning and evening flights to agricultural fields. Once these males began field feeding, use of loafing sites remained high but use of aquatic bed areas was incidental to moving off the loafing site prior to flying to agricultural fields.

Habitat Characteristics

Specific characteristics of the major cover types used by male mallards (Table 5) indicate all cover types had water depths which ranged between 28 to 47 cm. Species composition of the vegetative communities was relatively homogeneous with either cattail or bulrush dominating areas of emergent vegetation. Sago pondweed (Potomogeton pectinatus) was dominant in most aquatic bed areas (Table 5). Stem densities were highest in the bulrush cover type. Differences in horizontal vegetation density (Fig. 3) occurred between cattail and

Table 5. Characteristics of cover types used by radio-marked male mallards.

Cover Type	Water Depth (cm)	Species	Height (m)	Cover Percent	Stems/m²
Cattail (n = 21)	28 ± 1.7[a]	*Typha* spp.	2.4 ± 0.02	63 ± 2.9	62 ± 2.6
		Potamogeton pectinatus	---	3 ± 1.1	---
		Myriophyllum exalbescens	---	3 ± 0.8	---
Bulrush (n = 22)	38 ± 1.9	*Scirpus* spp.	1.4 ± 0.03	47 ± 2.7	152 ± 11.9
		Potamogeton pectinatus	---	2 ± 0.8	---
		Myriophyllum exalbescens	---	7 ± 1.0	---
Aquatic Bed (n = 21)	47 ± 1.3	*Potamogeton pectinatus*	---	96 ± 1.4	---
		Myriophyllum exalbescens	---	2 ± 0.7	---

[a]Mean ± standard error.

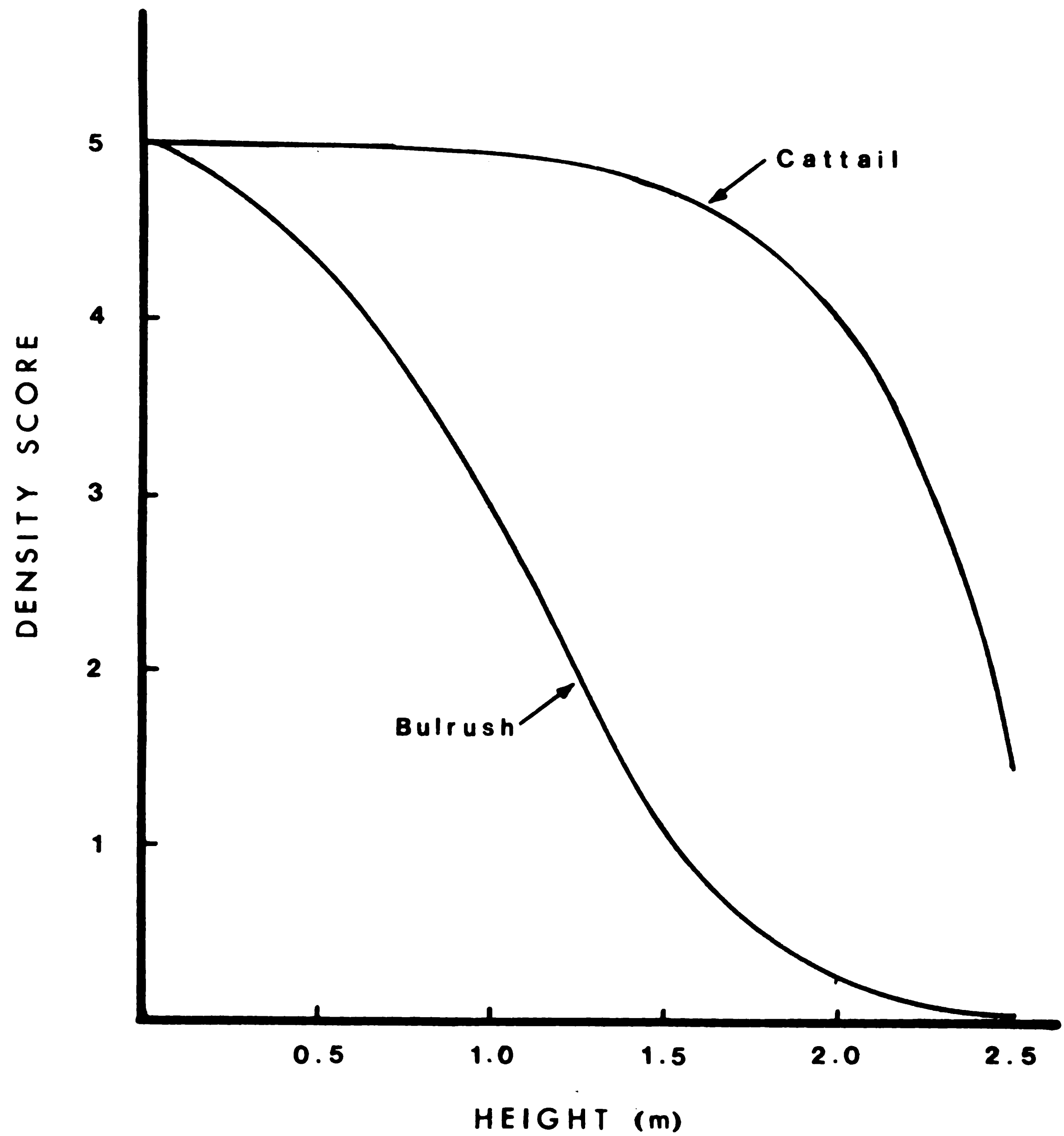

Fig. 3. Vegetation profiles for cattail and bulrush cover types. Density score units correspond to the number of quintiles at each height on a vegetation profile board (Nudds 1977). Differences in vegetation density are significant (p<0.001).

bulrush cover types ($p<0.001$).

The total number of cover type patches occurring within the utilization areas of preflightless, flightless, and postflightless males (Table 6) was not different ($T = 2.0761$, df=2, $P>0.05$). There were no differences in the number of aquatic bed ($T = 5.219$, df=2, $p>0.05$), cattail ($T = 2.076$, df=2, $p>0.05$), and bulrush ($T = 4.7428$, df=2, $p>0.05$) patches among groups as well. Approximately one-half of the total number of patches within the utilization areas of each group were aquatic bed and the other half were emergent vegetation indicating a high interspersion of cover types.

The average cover type patch length was different ($T = 8.6300$, df=2, $p<0.05$) among preflightless, flightless, and postflightless groups (Table 6). Utilization areas of flightless males had the smallest average patch length (90 m) and the smallest aquatic bed patch length (80 m, $T = 9.0777$, df=2, $p<0.05$). There were no differences detected in the patch lengths of cattail ($T = 5.4512$, df=2, $p>0.05$) and bulrush ($T = 0.9010$, df=2, $p>0.05$) and cover types among preflightless, flightless, and postflightless groups.

Table 6. Average number and length (m) of cover type patches occurring within utilization areas of postbreeding adult male mallards using the Delta Marsh, Manitoba.

Flight Category	Aquatic Bed				Cattail				Bulrush				Total[a]			
	Number		Length		Number		Length		Number		Length		Number		Length	
	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd
Preflightless	5	1	177[b]	49	2	2	66	60	2	0	64	4	8	2	137[b]	35
Flightless	4	1	80	25	2	1	112	44	1	1	71	44	8	2	90	24
Postflightless	4	2	189	127	3	2	225	171	2	1	84	49	9	3	172	67

[a] All cover type patches within each utilization area.

[b] Significant difference ($p<0.05$, Kruskall-Wallis Test) among flight categories.

DISCUSSION

Several habitat components emerged as being of significance to postbreeding male mallards. Open loafing sites were important for early preflightless and late postflightless mallards. These areas on the Delta Marsh were exposed mudflats or beaches formed of wave-washed plant fragments along the south edge of large open bays in the marsh. Flooded emergent cover was important to late preflightless, flightless, and early postflightless males. Emergent vegetation provided concealment as well as loafing sites, primarily in the form of accumulated fallen vegetation. Also, muskrat (*Ondantra zibethicus*) houses and abandoned over-water nests of American coot (*Fulica americana*) and western grebes (*Aechmophorus occidentalis*) within stands of emergent vegetation were frequently used as loafing sites. Bulrush and cattail are likely functional equivalents for concealment as horizontal vegetation densities up to 0.5 m above water surface are greater than 90% in both cover types. Shallow aquatic bed cover types were used predominantly as feeding sites. These areas often contained food items (e.g., sago pondweed) which did not occur in other cover types.

Utilization areas of preflightless ($\bar{x}$ = 21 ha), flightless ($\bar{x}$ = 6 ha) and postflightless ($\bar{x}$ = 43 ha) males using the Delta Marsh were much smaller than utilization areas or home ranges reported for breeding males. Gilmer et al. (1975) reported an average minimum home range of 240 ha for 12 males breeding in the Chippewa National Forest in northcentral Minnesota. Reduced utilization areas observed for postbreeding males can be explained on the basis of several factors. The size of an individual's utilization area at a particular point in the annual life cycle is related to the spatial and temporal distribution of required environmental resources and the ability to exploit those resources (Orians 1973, Schoener 1981). Mallard breeding pairs exhibit geographic variation in home range size which has been attributed to the quality and distribution of available habitat components (Gilmer et al. 1975:786, Dwyer et al. 1979:529). As one small wetland generally does not provide all of the requirements for a breeding pair (Dzubin 1969), use of a large utilization area encompassing diverse wetland types is advantageous (Dwyer et al. 1979:529). Postbreeding males face a reduction in mobility during the flightless period resulting in an upper limit in utilization area size which is lower than that for breeding males. The certainty of reduced mobility should favor the selection of habitats where all postbreeding requirements are in close proximity.

The juxtaposition of cover types used by postbreeding males on the Delta Marsh became increasingly important as individuals became flightless (Fig. 4). Preflightless and postflightless birds capable of flight were able to use desirable cover types even when not adjacent to each other. For example, 3 major loafing areas located on the south edge of large bays in the marsh had little food available in adjacent open water areas. Males using these areas, often several thousand, would fly to small potholes or wind protected channels and bays where aquatic bed areas and food items were available. Flightless males occupied smaller utilization areas where essential habitat

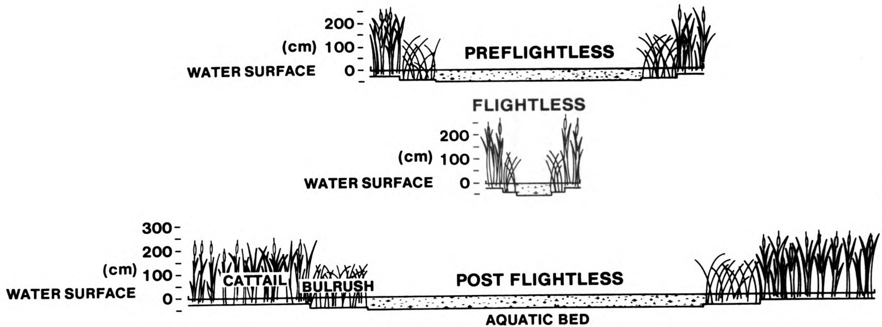

Fig. 4. Schematic comparison of wetland habitats used by postbreeding adult male mallards on the Delta Marsh. Profile diagram lengths are scaled relative to each other using average utilization area size and proportion of cover types within for males marked with radio transmitters.

components were adjacent. Mallard broods that are also flightless occupy home ranges similar in size (range = 4-20 ha) to those of flightless males (Talent et al. 1982).

Although postflightless males used aquatic bed areas extensively, and largely for feeding, this habitat use pattern apparently did not persist until migration. The reduction in aquatic bed use appeared to coincide with initiation of feeding in agricultural fields. This shift began in mid-August and continued through mid-September when our observations were terminated. The change in use of feeding habitats may represent a completion of the molt and is probably triggered by a change in a bird's physiological state from that of plumage growth to physiological preparation and commencement of fall migration.

Management Implications

Current marsh management objectives directed at waterfowl do not usually include recommendations for postbreeding concentrations. Consequently, postbreeding management goals need to be given consideration on areas which are typically managed for waterfowl production.

Recent studies (Weller and Fredrickson 1974, Bishop et al. 1979, Kaminski and Prince 1981, Murkin et al. 1982) have demonstrated the desirability of maintaining a "hemi-marsh" stage (cover:water ratio of 50:50) for breeding waterfowl. This can be accomplished through the management of emergent vegetation by a combination of waterlevel manipulation and/or muskrat management. While this management prescription is appropriate for breeding waterfowl, Murkin et al. (1982) indicate the role of the hemi-marsh outside of the breeding season is unknown.

Marsh management for postbreeding birds should provide situations having loafing areas and flooded emergent cover interspersed with adjacent shallow water areas containing desirable food items. The most appropriate cover:water ratio for a postbreeding marsh remains undefined at the present. A cover:water ratio of at least 50:50 seems preferable, particularly for flightless mallards. Experimental studies involving cover:water ratio manipulations are needed to better define the ratio. A further consideration relates to the differing spatial requirements of postbreeding birds. Specifically, flightless birds have a reduced utilization area and interspersion of emergent cover and open water containing food items must occur at a small scale.

The results of this study only provide insight into habitat requirements for postbreeding males once they have arrived on a postbreeding wetland. It appears that wetlands used by postbreeding male mallards are unique in the sense that they provide a combination of desirable habitat components in close proximity. The fact that most known postbreeding wetlands are large implicates wetland size as being important, although the nature of it's influence on use by postbreeding birds remains unknown. Furthermore, there is still little known about the movements of individuals from breeding to postbreeding areas and the environmental factors important at this time.

As wetland management intensifies in response to the continued development of our natural resources, a prioritization of the biological values of specific marshes may be necessary. For example, certain wetlands may receive most use by and be most valuable to postbreeding ducks. These marshes should be managed primarily for postbreeding ducks, rather than attempting to manage to benefit waterfowl during the breeding phase of the life cycle. Optimally, management of a marsh for breeding and postbreeding ducks may be possible if management strategies and results needed to benefit each group are not mutually exclusive.

CHAPTER II

FOOD USE OF POSTBREEDING MALE MALLARDS ON THE DELTA MARSH, MANITOBA

INTRODUCTION

Food habits studies of mallards (*Anas platyrhynchos*) have focused on breeding (Perret 1962, Swanson et al. 1979), migrating (Bossenmaier and Marshall 1958, Anderson 1959), and wintering periods (Wright 1959, Jorde et al. 1983). Sugden and Driver (1980) reported food habits for mallards using small wetlands in the Saskatchewan parklands during late summer and fall. However, food habits of mallards using large freshwater marshes during the postbreeding period have not been studied.

The postbreeding period is defined as the interval between involvement in reproductive activities and fall migration. Significant events occurring during the postbreeding period include plumage molt and growth, a period of flightlessness, and preparation for fall migration (Hochbaum 1944, 1955). Concurrently, there are shifts in patterns of habitat use (Hochbaum 1955, Gilmer et al. 1977) as adult males and reproductively unsuccessful females move to larger freshwater marshes during this period. These events dictate a set of environmental requirements which must be understood to evaluate the true impact of management recommendations and practices on dabbling ducks (Prince 1979). The purpose of this paper is to describe the diet of adult male mallards on the Delta Marsh, Manitoba during the postbreeding period.

STUDY AREA

The study was conducted on the 180-km^2 Delta Marsh located along the south shore of Lake Manitoba in southcentral Manitoba (50° 11'N, 98° 19'W). The marsh is characterized by dense stands of *Phragmites*, *Typha*, and *Scirpus* separating interconnecting large and small open water areas (Hochbaum 1944). Field activities were restricted to the East Marsh Unit between the villages of St. Ambrose and Delta. Descriptions of emergent vegetation are provided by Love and Love (1954), Walker (1959, 1965), and MacKenzie (1982). Submersed vegetative communities are described by Anderson and Jones 1976). Elson (1967) and Fenton (1970) report on physiography of the Delta Marsh.

METHODS

Adult male mallards were collected between May and September each year from 1981 to 1983. An attempt was made to collect equal numbers of birds within the preflightless, flightless, and postflightless stages (Gilmer et al. 1977) of the postbreeding period. Preflightless males were no longer paired, associated with a flock of other males, and had initiated the prebasic molt. Male mallards were classified as flightless if the wing cord measurement was less than 240 cm. Postflightless males were capable of flight and were in the mid- to late stages of the prealternate molt.

Collection techniques for preflightless and postflightless males were similar to those outlined by Swanson and Bartonek (1970). Flightless males were difficult to approach and collect by conventional methods due to difficult access to the marsh interior and the secretive behavior of the ducks. Consequently, flightless males were collected at night with a dip net from an airboat equipped with spotlights. All males collected were feeding in open water habitats. Esophageal contents were removed after collection and preserved in 80% ETOH for later analysis.

The feeding site of each male was sampled to determine food items available. Benthic food items were sampled using a core sampler similar to one described by Murkin et al. (1982). Swimming invertebrates were sampled using a 20.3 x 45.7 cm sweep net. Available aquatic vegetation and seeds used as foods were sampled following techniques of Anderson and Low (1976). Esophageal and food availability samples were sorted, and food items identified using Pennak (1953) and Merritt and Cummins (1978) for invertebrates; Martin and Barkley (1961) for seeds, and Fasset (1940) for vegetation. Food items were dried in an oven at 60° C for 48 h and weighed to 0.1 mg.

Data were summarized separately for the preflightless, flightless and postflightless groups, and presented as percent occurrance and aggregate (average) percentages (Swanson et al. 1974). Spearman rank correlation procedures (Conover 1971:335) were employed to examine relationships between the ingestion of specific food items. Comparisons of food use and availability were made using the ranking procedure of Johnson (1980) to assess food preferences.

RESULTS

Seventy-one adult male mallards were collected on the Delta Marsh. Food items were present in the esophagus of 16 of 18 preflightless males collected from 6 locations, 21 of 28 flightless males collected from 20 locations, and 22 of 25 postflightless males collected from 10 locations. Collections were made at accessible sites where feeding males were consistently observed. Preflightless and postflightless males used small shallow potholes situated in stands of emergent vegetation around the periphery of the marsh as well as small shallow bays and channels of the interior marsh. Flightless males were collected in shallow open water areas of the interior marsh which were dominated by dense stands of sago pondweed (Potamogeton pectinatus) and adjacent to dense stands of emergent vegetation.

Nine preflightless males were collected from small wetlands of the prairie pothole region near Minnedosa, Manitoba for comparative purposes. These birds represent postbreeding males which have yet to move to large marshes, such as the Delta Marsh, to undergo the molt process (Hochbaum 1944, 1955).

The diets of preflightless, flightless, and postflightless male mallards were dominated by plant matter (Table 7). Only preflightless males consumed a significant amount of animal matter. Nearly 66% of the aggregate dry weight was prairie bulrush (S. paludosis) seeds and Chironimidae and Culcidae larvae, but percent occurrence values

Table 7. Esophageal contents of postbreeding male mallards collected near Minnedosa, Manitoba and on the Delta Marsh, Manitoba during summer 1981-83. Sample size in parentheses.

	Minnedosa		Delta Marsh					
	Preflightless (6)		Preflightless (16)		Flightless (21)		Postflightless (22)	
Food Item	Aggregate % Dry Weight	Percent Occurrence	Aggregate % Dry Weight	Percent Occurrence	Aggregate % Dry Weight	Percent Occurrence	Aggregate % Dry Weight	Percent Occurrence
Plant Matter								
Potamogeton pectinatus (f)[a]	-	-	12.3	13	30.5	71	29.0	50
Potamogeton pectinatus (s)[b]	0.5	17	1.6	25	7.9	67	17.5	73
Potamogeton pectinatus (t)[c]	-	-	0.2	6	-	-	6.1	18
Potamogeton pusillus (s)	-	-	-	-	-	-	3.8	27
Zannichellia palustris (f)	-	-	6.0	13	-	-	12.4	23
Zannichellia palustris (s)	-	-	4.0	13	-	-	4.0	23
Scirpus acutus (s)	11.0	33	2.7	38	23.0	86	3.7	67
Scirpus validus (s)	-	-	-	-	-	-	0.6	22
Scirpus palidosis (s)	-	-	32.6	38	-	-	-	-
Polygonum amphibium (s)	-	-	0.1	13	-	-	-	-
Algae	-	-	-	-	3.7	5	1.3	5
Triticum aestivum (s)	76.2	83	-	-	-	-	-	-
Unidentified Plant Matter	tr.[d]	17	1.7	44	1.0	14	3.6	45
Total Plant Matter	87.7	100	61.2	100	66.1	100	82.0	100

Table 7 (con't.).

Animal Matter								
Gastropoda								
Planorbidae	-	-	0.2	38	6.2	52	2.1	32
Lymnaeidae	-	-	-	-	1.2	19	2.2	22
Physidae	-	-	-	-	0.1	5	0.2	14
Tricoptera	0.3	33	-	-	0.3	5	0.5	14
Odonata	2.3	17	-	-	-	-	0.3	5
Diptera								
Chironimidae	tr.	17	16.9	31	0.2	14	0.3	5
Culicidae	-	-	16.2	19	0.1	10	-	-
Hemiptera								
Notonectidae	-	-	-	-	0.5	5	-	-
Unidentified Animal Matter	-	-	0.1	19	0.3	10	3.1	50
Total Animal Matter	2.6	33	33.4	81	8.9	67	9.7	73
Grit	9.6	83	5.4	38	25.0	76	9.2	41

[a] Foliage

[b] Seed

[c] Tuber

[d] Tr. = <0.1%

were low. Two males collected from one location and 4 from another contained only prairie bulrush seeds in their esophagus. Three males from one site contained only Culicidae larvae, and 5 males from a different site contained only Chironimidae larvae. Another 2 males from an additional site contained predominantly horned pondweed (Zannichellia palustris) foliage and seeds. Sampling of food items available in the environment showed those food items selected were most available if not the only foods available at each feeding site.

The composite diet of the preflightless males collected in Minnedosa was composed of 88% plant material. Wheat formed the largest percentage (76%) and had the highest percent occurrence (83%) in the sample. Natural plant and animal food items occurred infrequently.

Sago pondweed foliage and seeds, and hardstem bulrush (S. acutus) seeds collectively comprised 61% of the diet of flightless males. Percent occurrence values for the 3 major food items ranged from 67 to 86%. Grit was found in 76% of the sample and it comprised 25% weight and 15% volume of the composite diet. Grit (dry weight) consumption was positively correlated with the consumption of hardstem bulrush seeds ($r_s = 0.43$, $P<0.05$). There was no correlation between consumption of sago pondweed foliage and grit ($r_s = -0.12$, $P>0.10$).

The frequency of occurrence was generally low for the food items found in the sample of postflightless males. This can be partially explained by the variation in availability of specific food items between collection sites. Although different food items may have been available from one site to another, e.g., dominated by sago pondweed or horned pondweed, the life form occurring in the diet (plant foliage and seeds) remained relatively consistent. Plant foliage comprised

41.4% of the diet and occurred in 73% of the sample. Plant seeds comprised 40.6% of the diet and occurred in 86% of the sample.

Estimates of food availability were made at the within feeding site level. Consequently, it was appropriate to test for food preferences using only males that had the same food items available at their respective feeding sites. Only the data for flightless males met this criteria. Application of Johnson's (1980) ranking procedure to the major food items consumed by flightless males revealed hardstem bulrush seeds to be preferred over sago pondweed foliage and seeds. The latter 2 food items were consumed in proportion to their availability.

DISCUSSION

The composite diet constructed from the sample of preflightless males collected on the Delta Marsh is likely not an accurate representation of the actual diet as the frequency of occurrence for all food items was low. This means that a composite description for this period will not predict individual consumption very well. Individual males which appeared to be in equivalent biological status (molt class) used very different food items, e.g., Chironimidae larvae versus prairie bulrush seeds. Food use was related to foods available at feeding sites rather than specific items that were sought, making it difficult to determine if food preferences existed for preflightless males in general.

The high proportion of wheat consumed by the sample of preflightless birds collected from the Minnedosa area further indicates the existence of high variability among individual males of equivalent status. Perret (1962:39) reported that 54% of the composite diet of 50 adult male mallards collected in the same area was composed of plant foods, 35% of which was cereal grains from agricultural fields. Animal foods composed 44% of the diet, the dominant taxa being Chironimidae larvae.

As flightless males were collected from many locations and all food items consumed were similarly available to all individuals, I feel the composite diet presented here is representative of flightless male mallards on the Delta Marsh. Invertebrate consumption is likely incidental to the consumption of sago pondweed foliage. The strong and positive relationship of grit and consumption of hard seeds was likely related to the need for grit in the digestive breakdown of foods.

The composite diet for postflightless males, at least the proportion of animal versus plant matter, appears to be a good approximation for those males feeding within the Delta Marsh. The high proportion of plant foods observed in the diet of postflightless males was similar to that observed in adult male mallards collected in August and September from wetlands in the Aspen-Parkland region near Saskatoon, Saskatchewan (Sugden and Driver 1980:706). Males collected on the Delta Marsh contained significant amounts of foliage from submergent macrophytes, specifically from sago pondweed and horned pondweed. The mallards in Saskatchewan did not contain this food item, although they did consume a vegetative plant part, duckweed (Lemna spp.). Consumption of sago pondweed seeds and tubers was similar for mallards in both studies. Invertebrate consumption by mallards in Saskatchewan was low, and percent occurrence values for specific animal food items were also low indicating consumption was highly variable among individuals in the sample.

My collections of postflightless males excluded those which were involved in field-feeding as did the sample of Sugden and Driver (1980). It appears that as males emerge from the flightless period they maintain a diet of natural foods and eventually make the transition to field-feeding on agricultural grains. However, how much of this diet shift is due to an active selection for different food items, possibly related to a change in physiological state from molting to preparation for fall migration, or a response to the sudden availability of an abundant food source is not clear.

CHAPTER III

ACTIVITY BUDGETS OF POSTBREEDING ADULT MALE MALLARDS ON THE DELTA MARSH, MANITOBA

INTRODUCTION

Adult male mallards (Anas platyrhynchos) experience both the prebasic and prealternate molt (Humphrey and Parkes 1959) during a 5 - 6 month period (Young and Boag 1982). This occurs immediately after breeding, making molt a major event of the postbreeding period (Hochbaum 1944, 1955).

Although not well studied, feather molt and replacement is considered a nutrient demanding process in birds (Payne 1972; King 1974). Individuals undergoing the molt process must be concerned with acquiring energy (King 1980) as well as certain sulphur amino acids (e.g. cystine) which are major components of feathers (Murphy and King 1982, 1984). Ankney (1979) proposed 3 nutritional stategies that molting birds may follow to meet the demands of molt: 1) increase daily nutrient intake; 2) make a compensatory reduction in other nutrient demanding functions (modify activity); and 3) catabolize body tissue (experience nutritional stress).

Body condition data for molting snow geese (Anser caerulescens) (Ankney 1979), mallards (Young and Boag 1982) and brant (Branta bernicla) (Ankney 1984) suggests these species do not catabolize body tissues and follow strategy 1: The nutrient demands of molt are adequately met by dietary intake. While these studies have provided non-experimental tests of strategy 3, there are no investigations providing empirical data to evaluate the validity of strategies

1 and 2 which relate to behavior. Activities of molting waterfowl remain largely unknown making it difficult to assess nutritional strategies exhibited during this period of the annual life cycle. In order to test the foregoing hypotheses, activity data was collected for postbreeding male mallards progressing through the prebasic-prealternate molt sequence.

STUDY AREA

This study was conducted on the 180-km^2 Delta Marsh located along the south shore of Lake Manitoba in southcentral Manitoba (50° 11'N, 98° 19'W). The marsh is characterized by dense stands of *Phragmites*, *Typha*, and *Scirpus* separating interconnecting large and small open water areas (Hochbaum 1944). Field activities were restricted to the East Marsh Unit between the villages of St. Ambrose and Delta. Descriptions of emergent vegetation are provided by Love and Love (1954), Walker (1959, 1965), and MacKenzie (1982). Submerged communities are described by Anderson and Jones (1976). The physiography of the marsh is described by Elson (1967) and Fenton (1978).

METHODS

Visual observations of preflightless and postflightless mallards were possible as activities were centered around open loafing sites and adjacent aquatic bed areas (open water dominated by submergent vegetation). Activities for these 2 groups were quantified using a modified scan-sampling technique (Altman 1974). Observations were made during 2-hour sampling periods randomly selected during diurnal hours (0500-2100 h). A predefined observation area was scanned continuously throughout each sampling period from an elevated blind using a 15-60 x spotting scope. Each individual mallard encountered during a scan of the observation area was considered a sample point. Activities were categorized as feeding, resting, swimming, flying, comfort movements, and alert.

A potential problem associated with the use of visual observation methods to quantify an activity budget is the inherent bias towards behaviors occurring in structurally open habitats. Behaviors occurring when birds are in dense cover are obviously not observed, being commonly recorded as out-of-sight, resulting in an incomplete activity budget. Since flightless mallards use areas of dense emergent vegetation extensively, visual observations were not used to collect activity data.

Activities of flightless mallards were quantified using a nasal-mounted radio transmitter. Flightless mallards were captured at night with a dip net from an airboat equipped with spotlights. Each male was fitted with a nasal saddle (Greenwood 1977), bearing a small radio transmitter and whip antenna. Transmitter signals were monitored using a fixed-point antenna, and signal strength (MHz) was recorded on paper tape using a Rustrack Strip-Chart Recorder connected to a radio receiver. This technique was validated by monitoring activities of pen-reared males fitted with the same radio package and held in a large flight pen placed in the marsh. A time-lapse camera was placed outside the pen to obtain a visual record of the activities of the penned males while transmitter signals were being recorded on a paper tape. Comparisons of film records with signal patterns on the paper tape revealed specific transmitter signal patterns for feeding, resting, and comfort movement activities were discernable. This method was not sufficiently sensitive to detect swimming and alert activities. However, casual observations of flightless birds indicated most swimming was directly associated with feeding activity and movements were not extensive. Alert behavior is generally not a sustained activity and was not detectable.

Data were summarized separately for preflightless, flightless, and postflightless groups. Chi-square analysis (Seigel 1956) was used to detect differences in activities among groups.

RESULTS

A total of 110 and 130 hours of visual observations were acquired for preflightless and postflightless male mallards, respectively. Five hundred thirty-one hours of behavior monitoring were recorded for 7 flightless males using nasal mounted radio transmitters. Observations of preflightless and postflightless males were restricted to diurnal periods while diel activity was obtained for flightless males.

Although the percent occurrence of activities differed between preflightless and postflightless males ($p < 0.0001$, $x^2 = 141.2$, df = 6), the level of all activities for both groups was similar (Table 8). Feeding and resting dominated the activity budget of both groups. Preflightless males spent more time swimming and less time involved in comfort movements than postflightless males. Flying occurred infrequently in both groups, and 2 and 1 percent of the diurnal period was spent alert by preflightless and postflightless males, respectively.

The activity budget of flightless male mallards (Table 8) was also dominated by feeding and resting. Comfort movements also occurred frequently in flightless males, however this value is likely inflated as it was not possible to separate out swimming behavior using the nasal radio technique. Feeding and resting behaviors were easily identified using the nasal radio technique and were not likely to be biased by the inability to separate out other behaviors. Flightless males spent more time feeding and resting and less time performing

Table 8. Percent occurrence of activities for postbreeding adult male mallards on the Delta Marsh, Manitoba during summer 1981-1983.

Activity	Preflightless[a]	Flightless[b]		Postflightless[a]
	Diurnal	Diurnal	Nocturnal	Diurnal
Swim	15	---	---	12
Fly	0	---	---	tr
Rest	31	36	44	34
Feed	40	34	39	35
Alert	2	---	---	1
Comfort Movements	13	30	18	17
Aggression	tr[c]	---	---	tr

[a]Visual observations.

[b]Nasal mounted radio data.

[c]Trace, less than 1%.

comfort movements during nocturnal hours ($p < 0.0001$, $x^2 = 567.67$, $df = 2$).

Statistical comparisons of activity budgets between flightless and preflightless, and flightless and postflightless males were not made due to the different method by which activity data was collected for the flightless group. Flightless males appeared to spend similar amounts of time feeding and resting in comparison to prelightless and postflightless males (Table 8). Comfort movements appeared to occur more frequently in flightless males although this value may be inflated and the magnitude of any difference is unknown.

Diurnal trends in the occurrence of activities were evident for preflightless and postflightless males (Fig. 5). Feeding activity was greatest in the early morning for both groups. Preflightless males showed a crepuscular pattern in feeding with a decline during midday and an increase in evening. This was not as evident for postflightless males as feeding activity throughout the diurnal period never decreased below 30%.

Resting and comfort movement activities followed a crepuscular pattern in preflightless males as well, and their occurrence appeared to be inversely related to feeding activity. Comfort movements and resting activity in postflightless males were lowest in early morning and increased in mid-morning, remaining nearly constant throughout the remainder of the diurnal period.

Swimming occurred at low levels thoughout the diurnal period for both preflightless and postflightless males. Swimming activity was highest in early morning and evening and was associated primarily with feeding activity.

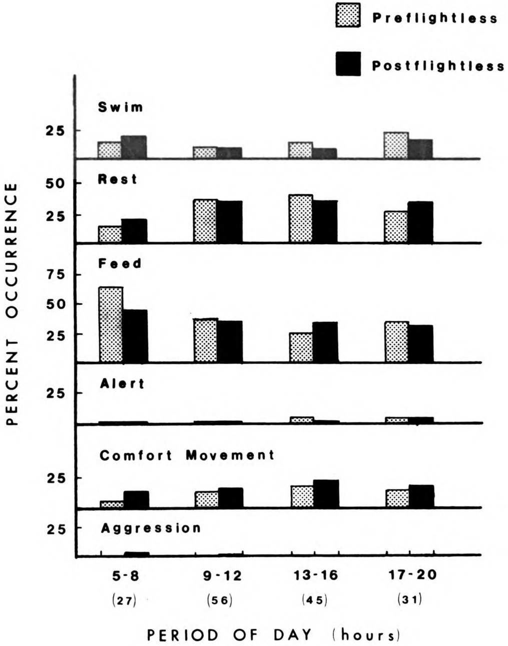

Fig. 5. Percent occurrence of activities for preflightless and postflightless adult male mallards using the Portage Creek concentration area during summer 1981 and 1983. Sample size in hours in parentheses.

Alert and aggressive behavior showed little diurnal variation. Alert behavior never exceeded 3%, and aggressive behavior was infrequent among preflightless and postflightless males.

Diel trends in activity were examined for flightless males (Fig. 6). Feeding activity occurred throughout the 24-hour period, the lowest levels occurring at mid-morning and midday. From late afternoon and through the night into early morning, feeding comprised 40% of the activity budget of flightless males. Comfort movements varied inversely to feeding activity, reaching their highest levels at midday and lowest levels during the night. Resting was the least variable activity of flightless males remaining near 40% throughout the diel period.

The relationships of activity to habitats occupied was examined for preflightless and postflightless males using the Portage Creek concentration area (Table 9). This was not possible for flightless males as the exact locations of individuals while involved in certain activities were not obtainable, either visually or via radiotelemetry. Due to the necessarily small size of the nasal-mounted radio transmitter, receiving range was usually less than 100 m. Consequently, accurate triangulations were not possible as the fixed-point antennas used for triangulations were not within this distance. Attempts to obtain locations using hand-held antennas were unsuccessful as flightless males were sensitive to approach within several hundred meters and would move as a result of the disturbance. Feeding activity was the dominant activity of males occupying aquatic bed cover types. Exposed mudflats were used predominantly for resting and comfort movements. Use of emergent vegetation cover types was less than 1 percent for

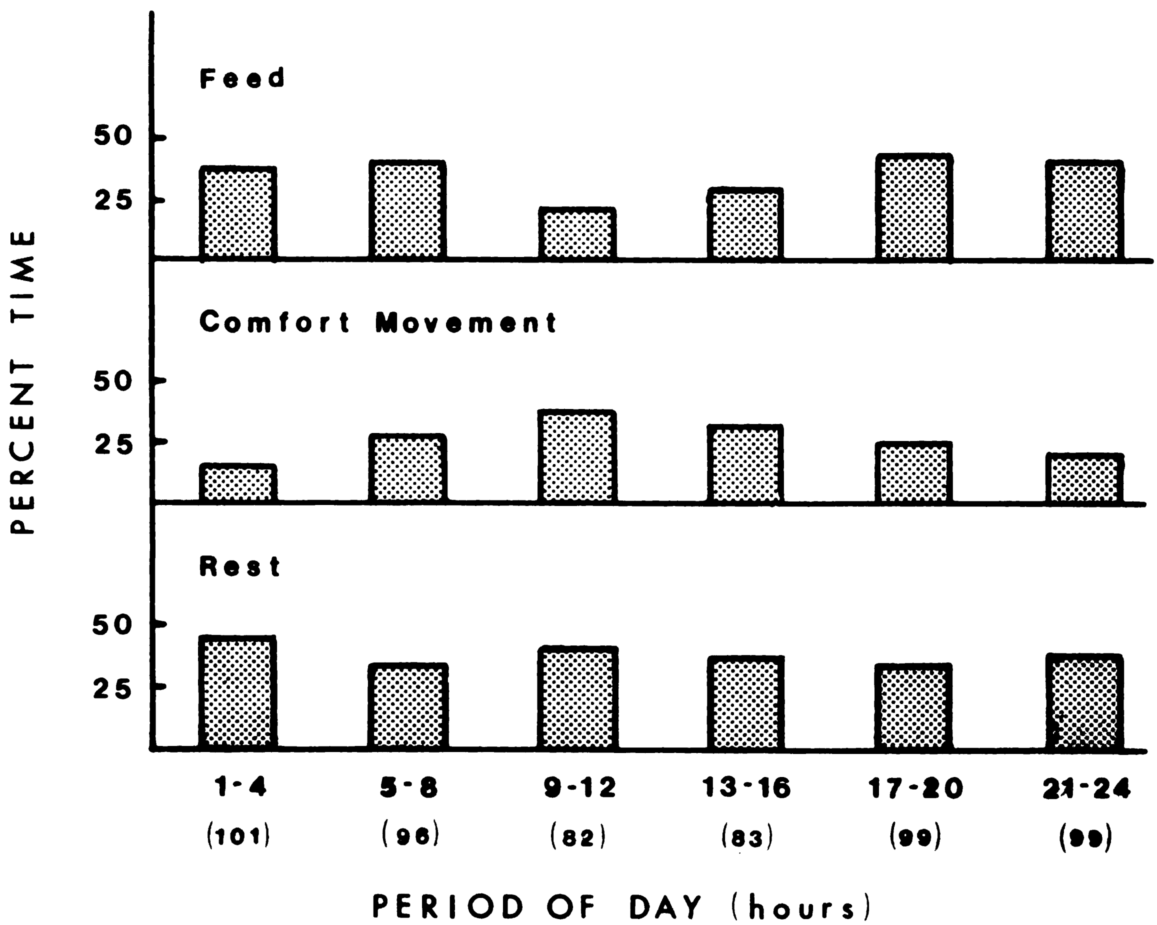

Fig. 6. Percent time spent in activities by flightless adult male mallards on the Delta Marsh, Manitoba during summer 1981 and 1983. Sample size in hours in parentheses.

Table 9. Percent occurrence of activities within major cover types for preflightless (n = 10253) and postflightless (n = 5527) adult male mallards using the Portage Creek concentration area on the Delta Marsh, Manitoba, during summer 1981-1983. Use of emergent vegetation cover types was less than 1 percent for both preflightless and postflightless males.

	Preflightless		Postflightless	
Activity	Aquatic Bed (n = 5867)	Mudflat (n = 4886)	Aquatic Bed (n = 3239)	Mudflat (n = 2284)
Swim	23	4[a]	18	2[a]
Rest	4	68	15	62
Feed	68	1	60	1
Alert	4	24	6	33
Comfort Movements	4	24	6	33
Aggression	0	0	0	1

[a]Individuals occupying shallow water at the mudflat-water interface.

both preflightless and postflightless males. Consequently, activities with this cover type were not examined.

DISCUSSION

Throughout the postbreeding period activity budgets of male mallards were dominated by feeding, resting, and comfort movements, respectively. The amount of time spent feeding by postbreeding males (approximately 40% of the diurnal period) is much higher than time spent feeding by paired males during the prenesting (14.7%), egg laying (20.0%) and incubation (8.7%) phases of the reproductive cycle (Dwyer et al. 1979). Titman (1981) reported levels of foraging for breeding male mallards similar to Dwyer et al. (1979). Postbreeding males spent more time involved in comfort movements and less time resting and alert than breeding males.

The observed changes in activity budgets as male mallards make the transition from breeding to postbreeding are undoubtedly related to changing nutrient demands which are a function of changing behavioral and physiological events. Postbreeding males no longer need to devote significant amounts of time and energy to alert and aggressive behavior as do breeding males . Such behavior provides breeding females with protection from predators and harassment from male conspecifics allowing increased feeding time (Derrickson 1977, Titman 1981). As mobility is reduced during the postbreeding period, nutritional demands are a result of maintenance or existence, plumage replacement, and fat deposition for fall migration. Males experiencing the molt process must be concerned with acquiring energy as well as certain sulphur amino acids. An expected increase in foraging for postbreeding males seems reasonable.

The greater amount of time spent performing comfort movements also is related to plumage replacement. Postbreeding males are involved in a nearly constant replacement of body contour feathers from June through September as they progress through the prebasic, remige, and prealternate molts (Young and Boag 1982). As male mallards continue to forage during molt, primarily in aquatic habitats, maintenance of the plumage for effective bouyancy remains critical. Increased attention to plumage during molt may be simply related to the comfort of the individual as well.

Molting male mallards appear to increase food intake, or at least feeding effort, and modify daily activity budgets from those observed for breeding males thus reducing the occurrence of nutrient demanding activities. The relative stability of net protein reserves in molting mallards (Young and Boag 1982) coupled with the high levels of feeding found in this study implicate an exogenous nutrient source is used to meet the nutritional demands of molt. However, a clear understanding of nutritional strategies exhibited by molting male mallards is still not possible due to a deficiency in our knowledge of how foraging time and effort interacts with diet composition and nutritional quality. Studies designed to investigate how diet quality and digestive efficiencies of specific food items influence molt are needed. This information when integrated with time-activity budgets and observed diets of wild mallards should help to elucidate nutritional problems and ecological strategies used to solve them.

CHAPTER IV

POSTBREEDING STRATEGIES OF MALLARDS

INTRODUCTION

The term "postbreeding" period has been used rather loosely by waterfowl biologists, sometimes including all events of the annual life cycle other than those related to breeding, or more appropriately the non-breeding period (Fredrickson and Drobney 1979). For the Anatini, the postbreeding period represents the interval between involvement in reproductive activities and fall migration. This is a biologically meaningful definition, especially for migratory species, as a specific set of physiological and behavioral events occur that can be separated from the breeding and wintering periods (Table 10).

Postbreeding adult male mallards progress through a prebasic molt, a simultaneous remige molt resulting in a 3 - 4 week period of flightlessness, and a prealternate molt (Weller 1976). Postbreeding female mallards experience the wing molt and flightless period, followed by the prealternate molt. Fledged young, in addition to being involved in growth, progress through a juvenile plumage, a prebasic molt, a short-lived basic plumage, followed by a prealternate molt into alternate plumage.

Subsequent to the flightless period, and over-lapping to varying degrees with the prealternate molt, adult mallards appear to enter a period of premigratory hyperphagia to accumulate fat reserves for fall migration (Young and Boag 1982). Young-of-the-year also likely experience this phenomena. Information concerning premigratory fattening

Table 10. Major phases of the annual cycle of Nearctic Dabbling Ducks (Anatini) and associated events.

Phase	Physiological Events	Behavioral Events
Breeding	Maintenance	Habitat Selection
	Photosensitivity	Predator Avoidance
	Gonadal Development	Pair-Bond Maintenance
	Egg Production	Incubation
	Developemnt of Brood Patch	Pair Break-Up
		Brood-Rearing
Postbreeding	Maintenance	Habitat Selection
	Juvenile Growth	Predator Avoidance
	Photorefractoriness	Gregariousness
	Plumage Molt and Growth	Secretive Behavior-
	Prebasic Molt[a]	Flightlessness
	Prebasic Plumage Growth[a]	
	Prealternate Molt[b]	
	Prealternate Plumage Growth[b]	
	Premigratory Hyperphagia	
Wintering	Maintenance	Habitat Selection
	Photosensitivity	Predator Avoidance
	Plumage Molt and Growth	Natural
	Prebasic Molt[c]	Human
	Basic Plumage Growth[c]	Gregariousness
	Premigratory Hyperphagia	

[a]Adult males and young of the year.

[b]Adult males, adult females, and young of the year.

[c]Females only.

and it's interactions with molt and migration in waterfowl is sparse (Owen 1970). However, there is substantial evidence suggesting premigratory fattening is a significant physiological event for other migratory avian species breeding in temperate regions (Wingfield and Farner 1980, Moore et al. 1982). Additionally, all individuals in the postbreeding phase must be concerned with activities related to immediate survival such as maintenance and predator avoidance.

POSTBREEDING STRATEGIES

Life history strategies exhibited by a species should evolve to maximize fitness, the sum of present reproductive success plus probable future reproductive success (Williams 1966, Schaffer 1974). While reproductive traits are an important component of fitness (see Stearns 1976, Bell 1980 for reviews), other factors may be of equal significance (Stearns 1976). Life history strategies observed during all phases of the life cycle, for example geographic distribution, habitat shifts, dispersal and dispersion have adaptive significance (Weller 1975). Since mallards are an iteroparus species, the postbreeding period should be viewed as contributing to fitness by insuring survival, enhancing future reproductive success and the opportunity for an individual to pass its genes on to succeeding generations (Fig. 7). An individual making a decision to enter the postbreeding phase in a given year is making a trade-off in allocation of productive energy to reproductive functions versus survival functions. This perspective of the postbreeding period in waterfowl provides a conceptual framework which is useful for elucidating the evolutionary development of the

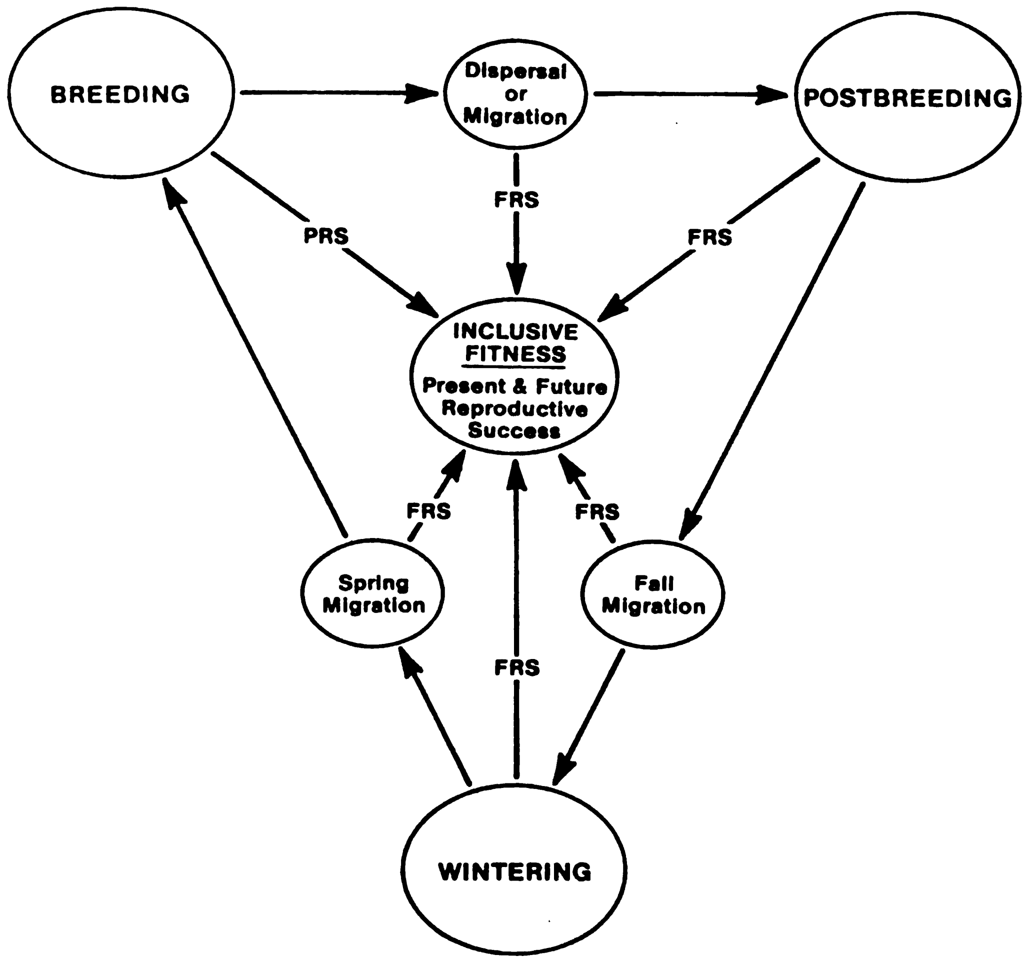

Fig. 7. The annual cycle of waterfowl in relation to present reproductive success (PRS) and future reproductive success (FRS) that contributes to the inclusive fitness of an individual.

mallard's life history strategy and for formulating effective management plans for the species. Several studies have suggested that events occurring during the non-breeding period may influence reproductive performance (Fretwell 1972, Raveling 1979, Heitmeyer and Fredrickson 1981). Consideration of the mallard's life cycle using the proposed model should facilitate a better understanding of the potential role of cross-seasonal influences.

The event of major significance during the postbreeding period is plumage molt and regrowth. Plumage renewal in waterfowl imposes a unique set of physiological demands and ecological constraints. For example, the simultaneous remige molt renders an individual flightless for an extended period of time. The change from an existence with high mobility to one of being relatively sedentary requires changes in habitat use patterns, behavior, and nutritional demands.

Breeding dabbling ducks have evolved in a highly dynamic and unpredictable environment, the prairie wetland ecosystem. Dramatic climatic fluctuations result in drought cycles affecting numbers and sizes of wetland basins annually and seasonally (Smith 1971, Stoudt 1971). Moreover, individual prairie wetlands may differ greatly in water permanence and habitat quality (Stewart and Kantrud 1971). Breeding ducks have adapted to this changing environment by using a "complex" of wetlands of differing habitat quality and water permanence in order to meet their requirements (Patterson 1976, Talent et al. 1982). Postbreeding dabbling ducks use relatively stable and more predictable wetlands habitats characterized as large shallow marshes (Hochbaum 1955, Sowls 1955, Salomonsen 1968, Oring 1964). Use of more predictable wetland environments during the postbreeding period affords several advantages enhancing survival. Plumage renewal and the accompanying flightless period dictates that an individual must be able to procure all of its requirements from a restricted area. Consequently, postbreeding individuals should utilize habitats which are more fine-grained (Orians 1973). My data for postbreeding male mallards lends support to this contention. Flightless males use wetland habitats where food and cover are in close proximity and little mobility is needed to utilize these resources. Certain large marshes or portions of them (e.g. Delta Marsh), consistently provide these habitat situations irrespective of annual or seasonal drought conditions which is often not the case for smaller prairie potholes used by breeding birds.

The selection of relatively stable and permanently flooded wetlands also may be important in the reduction of predation risks. The temporary reduction in mobility and escape ability due to flightlessness results in an increased probability of mortality if a predator is encountered. Flightless mallards appear to stay well within the interior of large wetlands avoiding terrestrial habitats and reduced encounters with terrestrial predators.

The secretive behavior exhibited by flightless mallards is viewed as an important tactic to further reduce predation risk (Hochbaum 1944, Salmonsen 1968, Gilmer et al. 1977). Even though use of large permanent wetlands affords some reduction in exposure to terrestrial predators, dabbling ducks still are subject to predation. My observations on the Delta Marsh during the summer indicate significant activity by both mink (*Mustela vison*) and great horned owls (*Bubo virginianus*) in areas where concentrations of flightless dabbling ducks occur. Extensive use of flooded emergent vegetation and nocturnal use of open water habitats (aquatic bed) further reduce exposure to predators. Flightless mallards on the Delta Marsh are usually solitary, or occur in small groups (<3). This may be an anti-predator behavior as being solitary in emergent cover facilitates hiding, whereas large groups attempting to hide would be a positive attraction to predators (Jarman 1974).

Differences in the timing of remige molt between adult male and female mallards exists. Reproductively successful, females are thought to delay molting activities until they leave their broods (Hochbaum 1944, Gilmer et al. 1977). Although timing of molt is likely controlled by a genetic program, the genome controlling molt is sensitive to extrinsic influences, mediated by the neuroendocrine system, within a moderate range of plasticity (Murphy and King 1984). For example, molt may be delayed by a late nesting cycle (King 1972, Bancroft and Woolfenden 1982) and may be postponed in individuals whose nesting season was prolonged by renesting caused by predation (Wingfield and Farner 1979). Thus, some flexibility in the timing of molt exists within the general time frame of the postbreeding period.

The difference in the timing of wing molt between male and female mallards offers an explantation for the molt migration (Salomonsen 1968) of males and non-breeding females from breeding areas (e.g. prairie potholes) to large marshes. Two hypotheses explaining postbreeding dispersal have been previously proposed. I refer to these as the food competition hypothesis (Salomonsen 1968) and the special habitat hypothesis (Hochbaum 1955, Gilmer et al. 1977).

The food competition hypothesis, if true, implies two assumptions. First, food resources are potentially limited on breeding areas.

Second, and most important, is that adult males, adult females, and young-of-the- year are competing for the same food resources at this time of the year. Fundamental to the validity of this hypothesis is a basic premise of competition theory. Biological competition is the demand by two or more individuals for a common ecological resource which is potentially limiting (Miller 1967). Food habits data for juvenile mallards indicate a high consumption of animal matter (Perret 1962) whereas postbreeding adult males appear to be opportunistic in food consumption making extensive use of plant matter. Thus an overlap in diet between adult males and young does not appear to exist which would invalidate the food competition hypothesis.

The special habitat hypothesis proposes the molt migration occurs as adult males and nonbreeders seek molting habitat which is unavailable on breeding areas. Two testable predictions exist if this hypothesis is plausible. Adult males should use habitat with different characteristics than what is available for breeding areas. Also, habitat used by adult males should be different than that used by adult females which remain on the breeding areas to molt.

While adult males move from breeding areas to large marshes this does not necessarily imply selection of a special habitat. Crucial here is the definition of habitat level. Certainly a large marsh differs from a prairie pothole in many respects, but the habitat actually being used may be only a small portion of the marsh having characteristics similar to habitats available on breeding areas. My data for flightless male mallards and observations of flightless female mallards (both successful and unsuccessful breeders) indicate both groups use habitats with the same characteristics which is non-supportive evidence for the special habitat hypothesis.

I propose a third hypothesis contending postbreeding strategies are adaptations to an unpredictable environment, enabling individuals to maximize their fitness by increasing the probability of future reproductive success. Of primary concern here, is the seasonal climatic fluctuation and its effect of prairie wetland water regimes. All prairie wetlands are not alike, water permanence being highly variable. The decline in pothole numbers and sizes from early spring through late summer is well documented (Smith 1971, Stoudt 1971). Millar (1969) found that less than 2% of the total number of wetland basins on study areas in Saskatchewan could be expected to hold water through the season in a year of average moisture conditions. The percentage of the total number of potholes containing water on May 1 still having water on August 1 varied from 98% to 25% during a 13-year study in the Alberta parklands (Smith 1971). Water dependent species have been forced to adapt to this changing environment in order to survive and reproduce.

Mobile individuals have the option of moving if and when a wetland drys. Individuals with restricted mobility, i.e., broods and flightless birds may face absence of cover and food resources, and increased vulnerability to predators. The existence of lethal brood areas is well established (Dzubin 1969, Smith 1971, Stoudt 1971). Smith (1971) has pointed out the inability of most breeding prairie waterfowl species to select seasonally permanent wetland habitats.

Adult male mallards leave females at the onset of incubation to undergo the prebasic molt and flightless period. At this point in time it is difficult to predict which wetlands will retain water through the summer as the seasonal precipitation evaporation trend is generally not established. Consequently, an individual electing to remain on the breeding areas at this time of year to undergo the flightless period has a high risk of selecting a pothole which will dry during the time of flightlessness. Therefore, it becomes advantageous and adaptive for mobile individuals (adult males and nonbreeders) to move to habitats with stable, or at least more predictable water regimes.

Evidence to date indicates reproductively successful females undergo the flightless period on wetlands on or in close proximity to the brood-reading wetland complex (Gilmer et al. 1977). Females with broods are committed to brood-rearing well into summer and do not become flightless until the brood is abandoned. Water permanence in a given wetland is more predictable at this time as the seasonal precipitation-evaporation pattern is established. Females are able to remain on breeding areas having a low risk of selecting a wetland which will dry at the time of flightlessness.

Falsification of the predictions derived from the special habitat hypothesis would lend support to this environemntal hypothesis. Moreover, it may be more appropriate to view the special habitat hypothesis as a corollary of the environmental hypothesis. The special habitat hypothesis concerns proximate factors of ecological causation, whereas the environmental hypothesis is based on ultimate factors. Stability and water permanence undoubtedly contribute to differences in habitat characteristics (vegetation structure, food availability, etc.) which are proximate factors eliciting either a positive or negative response to a particular habitat. The environmental hypothesis proposed here follows the model proposed by Patterson (1976) for breeding ducks. Patterson (1976) proposed that "the seasonal variations in the environmental requirements of the different life history stages of dabbling ducks to be an evolutionary adaptation to temporal environmental heterogeneity." Strategies observed during the postbreeding phase of the life cycle likely enable mallards to deal with the unpredictable prairie wetland environment as well.

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