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FOODS CONSUMED BY BREEDING MALLARDS ON WETLANDS OF SOUTH-CENTRAL NORTH DAKOTA

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Abstract: Foods consumed by 117 mallards (*Anas platyrhynchos*) collected on the breeding grounds of south-central North Dakota during spring and summer 1974–80 were examined. Animal foods accounted for 38 and 37% of the diet of paired males and nonlaying females, respectively ($N = 80$). The diet of laying females consisted of 72% animal foods, which differed significantly from that of paired males and nonlaying females. Insects, gastropods, crustaceans, annelids, and seeds made up 27.1, 16.4, 12.9, 12.8, and 24.8% of the diet, respectively, of laying females ($N = 37$).

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The prairie pothole region of North America contains a high density of shallow wetland basins with biotic communities that have developed under the influence of glaciation and a semiarid climate. Annual moisture deficits vary in magnitude and are accompanied by changes in water levels and dissolved salts (Stewart and Kantrud 1971, Swanson et al. 1974b). Plant and animal communities continually change in response to fluctuations in water level and salt content, and periodic droughts produce major changes in wetland biotic communities (Swanson and Meyer 1977). The dynamic nature of this water regime, and the periodic changes in the biota that it produces, is a dominant factor influencing the food base available to breeding waterfowl.

Superimposed on the dynamic water regime of the prairie pothole region are tillage practices that can alter seasonally flooded wetlands annually and semipermanent wetlands during drought years. Tillage alters the food base of low prairie, wet meadow, and shallow marsh zones and is a major factor interacting with hydrology to influence biotic succession and, consequently, food availability.

The high rate of nest destruction experienced by ground-nesting ducks in the prairie pothole region (Kirsch 1969, Higgins 1977) requires persistent renesting by mallard females if they are to achieve reproductive success. With each renesting effort and subsequent loss in body reserves, the food base available to breeding fe-

males increases in importance (Swanson et al. 1979).

Foods consumed by laying mallards on the breeding grounds have not been identified. Perret (1962) described foods consumed by mallard females, but the reproductive status of the birds was not reported. Some preliminary results of foods consumed by laying mallards were discussed by Swanson et al. (1979).

Studies of wetland ecology, mallard feeding ecology, and mallard renesting characteristics were undertaken concurrently in the prairie pothole region of south-central North Dakota to assess the ecological relation between breeding birds and their aquatic habitats. The purpose of the present paper is to describe foods consumed by laying female mallards on the breeding grounds of south-central North Dakota and compare these with foods of paired nonlaying females, paired males, and birds in autumn.

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METHODS

Actively feeding mallards were collected on cultivated, pastured, and idle wetlands in the drift prairie and Missouri Coteau of south-central North Dakota in 1974–80 (Swanson et al. 1974b). Wetland class, land use, and time were recorded at each feeding site. We sampled feeding sites with a net sweep (Swanson et al.

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Table 1. Proportion by volume of plant and animal foods in the esophagi of mallards collected during the breeding seasons of 1974–80 in south-central North Dakota.

Food	Male (39)		Nonlaying female (41)		Laying female (37)	
	Aggregate %	% occurrence	Aggregate %	% occurrence	Aggregate %	% occurrence
Total animal	37.6	56	37.0	66	71.9	86
Gastropoda	6.3	28	4.5	15	16.4	41
Lymnaeidae	4.1	26	0.1	10	11.4	35
Planorbidae	2.2	10	2.5	5	2.8	11
Insecta	16.8	41	22.6	57	27.1	62
Coleoptera	0.5	5	2.5	27	4.8	46
Diptera	10.0	21	12.6	29	6.0	30
Lepidoptera	—	—	1.5	10	2.8	5
Odonata	0.9	5	0.2	2	4.5	11
Trichoptera	5.3	18	5.7	10	8.7	14
Crustacea	11.3	23	7.5	27	12.9	30
Anostraca	0.4	3	2.6	10	4.2	14
Cladocera	2.9	8	—	—	2.6	5
Conchostraca	6.3	15	4.4	10	5.7	11
Amphipoda	1.7	3	—	—	0.4	3
Oligochaeta	—	—	—	—	11.8	16
Total plant	62.4	92	63.0	83	28.1	73
Seeds	56.4	90	58.5	66	24.8	70
<i>Chenopodium</i> spp.	0.7	5	2.3	10	—	—
<i>Ambrosia</i> spp.	1.6	5	2.6	12	2.9	5
<i>Helianthus annuus</i>	0.9	5	—	—	2.4	5
<i>Carex</i> spp.	1.8	8	0.4	7	—	—
<i>Scirpus</i> spp.	6.3	18	0.2	2	0.1	5
<i>Avena fatua</i>	2.4	3	—	—	—	—
<i>Echinochloa crusgalli</i>	18.3	28	22.8	32	5.9	16
<i>Glyceria</i> spp.	—	—	3.1	5	—	—
<i>Hordeum vulgare</i>	—	—	2.4	2	0.2	5
<i>Phalaris arundinacea</i>	—	—	—	—	2.7	3
<i>Setaria</i> spp.	1.8	15	5.3	17	1.0	5
<i>Triticum aestivum</i>	5.1	5	11.0	17	7.7	11
<i>Zea mays</i>	2.2	3	2.2	2	—	—
<i>Polygonum</i> spp.	10.1	31	1.1	2	0.3	8
<i>Rumex</i> spp.	2.6	8	1.0	5	0.4	5
<i>Potamogeton</i> spp.	—	—	2.4	7	—	—
Vegetation	6.0	15	4.5	13	3.3	8
Roots and tubers	4.1	5	3.9	12	2.8	5

1974b), core sampler (Swanson 1978a), and water column sampler (Swanson 1978b).

Males paired with females were collected whenever possible to obtain both birds on the same feeding site. Esophageal contents were removed, sorted, measured volumetrically, and tabulated by methods described by Swanson et al. (1974a,b). Females were classified as laying if they contained an egg in the oviduct or recently ruptured follicles.

Esophagi of hunter-killed birds were examined in the autumn of 1974–76 to compare foods consumed by autumn migrants with those of breeding birds. Autumn mallards were shot on wetlands by decoying or jump shooting. Co-

operators were instructed to process birds in a prescribed manner to reduce postmortem digestion and decomposition.

Animal foods in the diet of males, nonlaying females, and laying females were compared by a one-way analysis of variance (ANOVA) and Duncan's Multiple Range Test.

RESULTS

The invertebrate content in the diet of laying females, nonlaying females, and paired males differed ($P < 0.001$, one-way ANOVA). Consumption of invertebrates by laying females was greater than that of paired nonlaying females and paired males ($P < 0.05$, Duncan's Multiple

Table 2. Proportion by volume of plant and animal foods in the esophagi of 37 laying mallards collected during the breeding seasons of 1974–80.

Food	Apr (10)		May (19)		Jun ^a (8)	
	Aggregate %	% occurrence	Aggregate %	% occurrence	Aggregate %	% occurrence
Total animal	67.8	80	66.8	84	89.4	100
Gastropoda	tr ^b	10	24.9	58	16.5	38
Lymnaeidae	—	0	24.5	58	4.1	25
Insecta	13.1	30	25.6	68	48.1	88
Coleoptera	1.2	20	6.5	58	3.8	38
Diptera	1.8	20	10.2	37	4.3	38
Hemiptera	—	—	0.1	11	0.1	—
Lepidoptera	10.0	10	0.1	5	—	0
Odonata	0.1	10	tr	5	20.4	25
Trichoptera	—	0	8.7	0	19.5	25
Crustacea	7.9	20	15.1	37	13.9	25
Anostraca	6.4	10	4.8	21	—	0
Cladocera	—	0	0.5	5	11.0	13
Conchostraca	—	0	9.8	16	2.9	13
Annelida	38.3	50	0.2	5	10.9	13
Oligochaeta	34.9	50	—	0	10.9	13
Hirudinea	3.4	10	0.2	5	—	0
Miscellaneous animal	8.5	10	1.0	16	—	0
Total plant	32.2	90	33.2	74	10.6	50
Seeds	28.7	90	28.7	68	10.6	50
Tubers	2.4	10	4.3	5	—	0
Stems	1.1	10	0.2	5	—	0

^a Includes birds collected in the 1st week in July.

^b tr = <0.1.

Range Test). The proportion of invertebrates in the diet of nonlaying females and males, however, did not differ significantly.

The diet of laying females included the following percentages: insects, 27.1; gastropods, 16.4; crustaceans, 12.9; annelids, 12.8; and seeds, 24.8 (Table 1). *Lymnaea* spp. were dominant mollusks consumed. Trichoptera, Diptera, Coleoptera, and Odonata made up 8.7, 6.0, 4.8, and 4.5% of the diet, respectively. Conchostraca and Anostraca were the dominant crustaceans in the diet, accounting for 5.7 and 4.2%, respectively. *Triticum aestivum* and *Echinochloa crusgalli* were the seeds most often consumed by laying females, accounting for 7.7 and 5.9% of the diet, respectively. *Echinochloa crusgalli* was the dominant seed in the diet of nonlaying females and males and made up 22.8 and 18.3% of their diet, respectively.

Seasonal trends in the diet of laying female mallards reflected hydrological and phenological events that influenced availability of foods (Table 2). During April, animal foods accounted for 68% of the diet. Gastropods were consumed in only trace amounts. Insects were represented by terrestrial Lepidoptera larvae that drowned when seasonally flooded wetlands filled

with water during snowmelt. Crustaceans were represented by Anostraca, which are the first aquatic invertebrates to mature in recently flooded temporary and seasonal wetlands. Terrestrial oligochaetes, stimulated by early spring rains to migrate to the surface, accumulated in shallow ephemeral pools and accounted for 35% of the April diet.

Invertebrates made up 67% of the diet of laying females in May; annelids accounted for <1% of the diet. Conchostraca and Anostraca, which inhabit shallow marsh and wet meadow zones, were the dominant crustaceans consumed. Gastropods found in trace amounts during April accounted for 25% of the foods consumed during May. Aquatic insects made up 26% of the May diet.

Invertebrates dominated the diet of laying females during June and early July, accounting for 89% of the foods consumed. Odonates and Trichoptera each made up 20% of the late spring and early summer diet. Cladocera replaced Anostraca and Conchostraca, reflecting the response of mallards to the loss of seasonally flooded wetlands and a shift in feeding to semi-permanent lakes.

The influence of annual water regimes on

feeding ecology was demonstrated in the spring of 1977. Seasonal wetlands were dry, semipermanent lakes were in drawdown, and the shallow marsh and wet meadow zones usually available to mallards during spring and early summer were dry. Mallards responded by feeding in open water zones on semipermanent lakes along the edge of mud flats that developed on the outside of the deep marsh zone. This change in hydrologic conditions was reflected in the aquatic foods consumed. Oligochaetes were absent from the diet. Anostraca and Conchostraca associated with shallow marsh and wet meadow zones were replaced by pelagic Cladocera found in the open water of semipermanent wetlands. Benthic insects dominated the diet, accounting for 48% of the foods consumed. Chironomids and Trichoptera made up 26 and 16% of the diet, respectively. *Helisoma trivolvis*, a planorbid snail found in permanent and semipermanent lakes, replaced *Lymnaea* spp. Tubers exceeded seeds, accounting for 21% of the foods consumed.

The loss of temporary and seasonal wetlands and the temporary and seasonally flooded zones of semipermanent wetlands stimulated competition for the available feeding sites on drawdown zones and initiated intraspecific strife between mallard pairs. Female mallards were observed to join flocks of males during June 1977. In contrast, during the wet spring and summer of 1975 and 1979, females continued to renest into late June and early July, and the flocks of males observed did not contain females until July. Laying females were collected as late as July only during 1975 and 1979.

Laying females accounted for 51% of the paired females examined during the breeding season and ranged from 40% in early July to 55% in May. The presence of laying females throughout the nesting season indicates a strong renesting effort.

Ephemeral, temporary, seasonal, and semipermanent wetlands accounted for 12, 20, 44, and 24%, respectively, of the wetland classes utilized by birds examined during the breeding season.

Plant foods dominated the diet of 53 males and 20 females examined during the autumn of 1974–76. Seeds accounted for 86 and 100% of the male and female diet, respectively (Fig. 1). *Triticum aestivum* dominated the foods of birds in the autumn (73%).

Small grains dominated the diet of birds shot

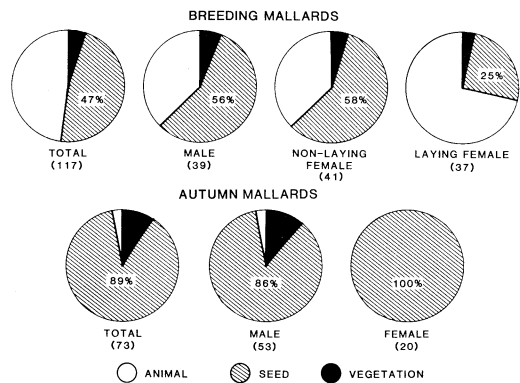


Fig. 1. Proportions of animal, seed, and vegetation consumed by mallards during spring, summer, and autumn in south-central North Dakota, 1974–80.

over water during autumn 1974–76 in south-central North Dakota when cereals were highly available and seasonal wetlands were dry. During years when late summer precipitation refilled seasonal wetlands and caused waste grain in the upland to germinate, mallards altered their feeding behavior and fed on seasonal wetlands where they consumed root stocks and seeds. Autumn mallards also fed on *Potamogeton pectinatus* tubers that were available in shallow semipermanent wetlands (G. A. Swanson, unpubl. data).

Three-year-old wild-strain mallards placed on experimental ponds and provided an unlimited food supply responded to imposed nest destruction by producing four and five clutches of eggs during the breeding season (Swanson, unpubl. data). When food availability was reduced on experimental ponds, mallards extended their renesting intervals. Mallards on experimental ponds provided with an abundant food base and incubating up to 14 days renested in 6 and 7 days in response to imposed nest destruction.

DISCUSSION

Factors Influencing Food Selection

Foods selected by mallards are influenced by the physiological requirements of the bird and their morphological adaptations for feeding (Swanson et al. 1974b). Mallards, like other dabbling ducks, are morphologically adapted to feed in shallow water or close to the water surface (Zweers et al. 1977). Feeding zones are altered by changes in depth, and invertebrates move in and out of the zones as they respond to changing environmental conditions (Swan-

son 1977, Danell and Sjöberg 1982). Invertebrate foods associated with the water surface include emerging insects; insects, mollusks, and crustaceans attached to aquatic substrates near or on the water surface; and pelagic crustaceans and insects that periodically migrate to the water surface. Availability of surface-associated invertebrates is influenced by changes in climatic conditions (Swanson and Sargeant 1972, Swanson and Meyer 1977, Sjöberg and Danell 1982).

Foods available to mallards as they arrive on the breeding grounds are waste grain and seeds such as those of *E. crusgalli* that are found in shallow wetlands created by snowmelt. As the frozen ground thaws, ephemeral wetlands dry and warm spring rains stimulate oligochaetes to move to the surface where they often accumulate in shallow wet depressions. As the spring season progresses, the species of invertebrates available for consumption by breeding mallards changes (Dement'ev and Gladkov 1967: 459, Swanson et al. 1974b). Early developing species of Anostraca complete their life cycle in April and are replaced by Conchostraca, insects, and mollusks. Invertebrate abundance and availability in temporary and seasonal wetlands remains relatively high during the period that water is present (Swanson et al. 1974b).

As summer progresses, submerged vascular plants in the open water zones of semipermanent lakes and littoral areas of perennial lakes approach the water surface and provide a substrate for invertebrates such as mollusks, chironomid larvae, and amphipods. Diptera and Ephemeroptera also emerge from the water surface and provide an abundant, highly available food source (Swanson and Sargeant 1972, Swanson 1977, Danell and Sjöberg 1982).

Paired mallards took advantage of newly created wetland habitat when late spring rains filled dry seasonal wetlands on the drift prairie. Paired females that occupied newly created wetlands in 1979 contained rapidly expanding follicles or eggs in their oviduct. Because the birds were new arrivals to the immediate area that was previously dry, it was assumed that they were previously unsuccessful and were responding to reneest in June and early July on the newly created aquatic habitat. High use was made of shallow depressions that often held water for only a few days. Foods consumed under these conditions were *E. crusgalli*, small gastropods that aestivate during dry periods, invading adult

insects, and rapidly developing insects and crustaceans such as Culicidae and Conchostraca.

The number of shallow wetlands available during the breeding season varies annually and influences the total food base. Temporary and seasonal wetlands account for 34 and 61% of the wetland surface area in the Missouri Coteau and Drift Plain, respectively, in central North Dakota (Cowardin et al. 1981). During dry years, the wet meadow, shallow marsh, and deep marsh zones of semipermanent lakes also are dry, further reducing the wetland surface area available to breeding waterfowl.

In dry years, mallards are restricted to feeding on drawdown zones within the deep marsh or open water zones of semipermanent and permanent lakes. In the dry spring of 1977, birds were forced to feed on semipermanent wetlands in drawdown. Mallards concentrated on a reduced number of wetlands that contained an abundant benthic invertebrate population, and conflicts over space intensified three-bird chases. Social interactions that occur when high quality wetland habitat is reduced in dry years cause birds to expend stored energy reserves that would otherwise be available for egg production. A female with an aggressive drake that repels other pairs permitting her to feed undisturbed has a distinct advantage (Titman 1981). When pursuing males completed a three-bird chase, they were observed to return to the site where their mate continued to feed undisturbed.

Physiological Response

As nest losses increase on the breeding grounds, breeding females must depend on natural wetlands to provide the high protein foods required to support their reneesting efforts. Weight loss as the breeding season progresses depletes stored body reserves that can be mobilized for egg production (Dwyer et al. 1979; Krapu 1979, 1981; Street 1981). Dwyer et al. (1979) found that female mallards increased the time devoted to feeding from 18 to 55% from preneesting to laying. As weight loss occurs with each reneesting attempt, foods that replenish lost body reserves increase in importance (Krapu 1979).

Mallards persistently reneest when high protein foods are highly available. Titman (1981) documented an 8-day reneesting interval in the field following the destruction of a mallard

clutch that had been incubated for 8 days. The mallard female observed by Titman (1981) produced three clutches during the breeding season. Krapu (1979) reported that radio-marked mallard hens monitored in south-central North Dakota made up to four nesting attempts. The low rate of nest success reported on agricultural lands in the prairie pothole region (Cowardin and Johnson 1979) suggests that a high proportion of successful mallard clutches are the product of re-nesting efforts. The high proportion of paired females that are laying throughout the breeding season suggests that a high rate of re-nesting by female mallards occurs in the prairie pothole region.

Pospahala et al. (1974) reported a significant relationship between the late nesting index and the number of July ponds each year in the prairie-parkland area. They reported that re-nesting efforts seem strongest during years when mid-summer water conditions are good. When temporary and seasonal wetlands contain water during the nesting season, abundant, high protein foods are available to support a strong re-nesting effort. In contrast, during drought years the loss of preferred feeding zones reduces the food base that is available to support re-nesting. As wetland complexes in the prairie pothole region are altered by drainage and siltation, the aquatic food base available to support re-nesting can be expected to decrease.

MANAGEMENT IMPLICATIONS

Knowledge of the ecological factors that influence the aquatic food base of wetlands, the reproductive requirements of breeding waterfowl, and the response by breeding birds to changing wetland conditions provide a data base that can be used to develop guidelines for managing wetlands. Impoundments constructed for waterfowl on the breeding grounds of North America and natural lake basins that have water management capabilities can be manipulated to provide hydrologic regimes and chemical conditions that support foods that are attractive to breeding waterfowl. Management strategies that duplicate the hydrology, basin morphology, and chemistry of wetlands in a prairie wetland complex will provide ideal aquatic habitat for breeding mallards.

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DIET AND NUTRITION OF BREEDING FEMALE REDHEAD AND CANVASBACK DUCKS IN NEVADA

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Abstract: Diet, nutrition, and foraging strategies of breeding female canvasback (*Aythya valisineria*) and redhead ducks (*A. americana*) were studied by collecting foraging birds in 1980 and 1981 at Ruby Lake National Wildlife Refuge (Ruby Lake NWR). Female canvasbacks consumed a small number of food items, most of which were not abundant in the marsh. The diet of redheads changed with each stage of the reproductive cycle; they usually foraged on the most abundant foods in the marsh. Nutrient and energy content of the diet of canvasbacks varied little from laying through brooding, but both were quite variable in the diet of female redheads. Female canvasbacks retained large lipid reserves during formation of the clutch but used 68% from late laying to the incubation stage. Redheads expended 46% of their lipid reserves during formation of the clutch and 30% from late laying to incubation.

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Food habits and changes in body reserves of breeding waterfowl have received much attention, especially for dabbling ducks (*Anas* spp.) (Krapu 1974, 1981; Swanson et al. 1974b; Serie and Swanson 1976), wood ducks (*Aix sponsa*) (Drobney and Fredrickson 1979), and geese (*Chen*, *Branta*) (Harwood 1977; Ankney and MacInnes 1978; Raveling 1979). Generally, lipid reserves are accumulated before laying as a result of consumption of plant foods high in carbohydrates. During laying, females feed on foods high in protein (invertebrates by ducks, sprouting grasses by geese) to supply the protein necessary for egg production, and begin to utilize their lipid reserves. Restriction of food intake during incubation results in rapid depletion of lipid reserves. By the end of the incubation period, females have nearly exhausted their lipid reserves. The diet and nutrient cycles

of breeding diving ducks (*Aythya* spp.), which feed to a greater extent on animal foods throughout the year than do dabbling ducks (Cottam 1939, Martin et al. 1951), have not been reported.

We investigated the relationship between diet and body reserves of two closely related species of diving ducks, the redhead and the canvasback. These two species occur together over much of their range and have similar habitat requirements during the breeding season (Weller 1959). However, they pursue different nesting strategies: the redhead is semiparasitic, whereas the canvasback is not (Weller 1959). Thus, their foods and nutrient cycles during the breeding season might be expected to be different, even when both species occur in the same marsh.

The objectives of this study were to: (1) determine the foods consumed, preference for foods, and nutrient content of the diet of female canvasbacks and redheads; (2) determine changes in body weight and body reserves dur-

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