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FOODS AND DIETARY STRATEGIES OF PRAIRIE-NESTING RUDDY DUCKS AND REDHEADS[1]

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Abstract. Actively feeding Ruddy Ducks (*Oxyura jamaicensis*) and Redheads (*Aythya americana*) were collected from North Dakota wetlands during the 1979–1981 breeding seasons. Foods found within esophagi were analyzed on a wet-weight aggregate percent basis. Male and prelaying and laying female Ruddy Ducks consumed >90% invertebrates, primarily chironomids. Postlaying female Ruddy Ducks consumed 73% invertebrates. Male and female (prelaying, laying, and postlaying) Redheads were consistently more omnivorous, consuming 51–70% invertebrates (mostly chironomids) and 30–49% plant matter. Seeds of shallow marsh emergent plants were important in the diet of prelaying and laying female Redheads in 1979, a wet year. Female Redheads used temporally available seed resources in shallow marshes to meet energy requirements for foraging on invertebrates in deeper, more permanent wetlands. Continued losses of easily drained shallow wetlands may represent a serious impediment to our efforts to maintain current Redhead population levels.

Key words: *Ruddy Ducks;* Oxyura jamaicensis; *Redheads;* Aythya americana; *prairie-nesting; foods; dietary strategies.*

INTRODUCTION

Food resources are the key to avian reproductive success (Marshall 1951, Lack 1954). Among Anseriforms, Snow Goose (*Chen caerulescens*) and Canada Goose (*Branta canadensis*) clutch sizes probably are determined by available body reserves, which are a function of late-winter and migratory staging area food resources (Ankney and MacInnes 1978, Raveling 1979). The importance of food for successful reproduction also has been demonstrated for Mallards (*Anas platyrhynchos*). In this species, female nutrient reserves (Krapu 1981), egg weight, hatchability, and potentially, duckling survival (Krapu 1979) are affected by quality of foods available to females. Diving duck reproductive effort and success also are known to decline in areas with reduced food resources (Bengtson 1971, 1972; Bengtson and Ulfstrand 1971).

Our understanding of the importance of food resources for waterfowl reproductive effort and productivity has evolved from a series of research efforts (summarized in Swanson et al. 1979) which focused on the feeding ecology of dabbling ducks breeding in the prairie pothole region (PPR). Little is known of the foraging ecology of breeding diving ducks in the PPR, although for some diving ducks, basic food habits (Bartonek and Hickey 1969, Siegfried 1973) and bioenergetics (Tome 1984) have been documented. Ruddy Ducks (*Oxyura jamaicensis*) and Redheads (*Aythya americana*), two abundant diving ducks in North Dakota and elsewhere in the PPR (U.S. Department of Interior 1987), were chosen for a comparative foraging ecology study. Interspecific comparisons, as demonstrated by Lack (1968) and discussed by McKinney (1978), are superior to single-species studies because they provide additional insight into ecological and evolutionary questions. The objectives of our study were to (1) compare diets of breeding Ruddy Ducks and Redheads, (2) determine if male and female (prelaying, laying, and postlaying) diets differ within species, and (3) relate dietary strategies to implications for potential conservation efforts.

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STUDY AREA AND METHODS

The study was conducted in 1979–1981 near Jamestown, North Dakota. We observed birds feeding at least 10 min before collecting them by shotgun. Many wetlands contained water in 1979, and we collected birds from 28 wetlands. Because of drought in 1980–1981, birds were collected from only 15 wetlands in 1980 and four in 1981. Collecting in 1981 was concentrated on wetlands where both species were present. Numbers of wetlands from which both species were collected, and range of elapsed collecting time for individual wetlands, were as follows: two wetlands in 1979, range = 0–3 days; nine wetlands in 1980, range = 1–15 days; three wetlands in 1981, range = 6–28 days.

Following collection, esophageal contents were removed, washed, and bottled in 80% alcohol for storage and later quantification. We processed esophageal contents in the laboratory by using a counting wheel (Swanson and Thornsberry 1975). We identified most animal matter to invertebrate family and plant matter to genus. Identification was according to: Ross (1944), Usinger (1956), Pennak (1978), Biosystematics Research Institute (1981), and Merritt and Cummins (1984) for invertebrates; Martin and Barkley (1961) for seeds; and Fassett (1957) for vegetation. Foods were weighed to the nearest 0.01 g and then expressed on an aggregate percentage wet-weight basis (Swanson et al. 1974a). Only birds containing ≥ 0.05 g esophageal contents were included in the diet composition analysis.

After removal of gastric contents, bird carcasses were placed in plastic bags and frozen. Reproductive organs were preserved intact in the frozen carcasses before removal for assessing the reproductive stage of females. We assigned females to reproductive categories of (1) prelaying, (2) laying, and (3) postlaying on the basis of reproductive tract appearance and condition (modified from Krapu 1974). The few females that had been initiating renesting but had not yet begun laying (based on ovary appearance) were assigned prelaying status.

Because proportions of invertebrates, seeds, tubers, and vegetation were distributed differently in Ruddy Duck and Redhead diets, interspecific comparisons (except for tubers) were made with the Mann-Whitney *U*-test and Wilcoxin's signed-rank test. Only eight birds consumed tubers, so the median test (Conover 1971) was used to compare tuber proportions in Ruddy Duck and Redhead diets. We also used the median test when comparing the number of invertebrate orders, insect families, and plant families consumed by Ruddy Ducks and Redheads. Because of non-normally distributed data within species, we employed the logistic transformation on food proportions in diets to accommodate use of parametric statistical techniques. Within-species comparisons between reproductive groups were made with one-way ANOVA.

RESULTS

RUDDY DUCK FOODS

Ruddy Duck diet composition was determined from 82 adults (37 males, 45 females), of which 77 were collected from Class IV, three from Class V, and two from Class III wetlands (classification from Stewart and Kantrud 1971). Ruddy Ducks were carnivorous, as invertebrates constituted 92% (89% macro-invertebrates and 3% micro-invertebrates) of foods. Insecta was the most important invertebrate class, constituting 78% of the overall diet and 85% of all invertebrates. Chironomidae (Insecta: Diptera) larvae and pupae were the major component of overall diet (72%), total invertebrates (78%), and total insects (92%). Plant matter composed 8% of Ruddy Duck foods. Plant foods were seeds (4%), pondweed (*Potamogeton*) tubers (2%), and vegetation (2%).

RUDDY DUCK DIETS BY REPRODUCTIVE CATEGORIES

Male and prelaying, laying, and postlaying female Ruddy Ducks did not consume invertebrates in equal proportions (F-test, df = 3,78, $P < 0.025$). Males consumed 91% invertebrates (Table 1), most (95%) of which were insects. Male Ruddy Ducks specialized during the breeding season on Chironomidae, which constituted 85% of the overall diet, 93% of all invertebrates, 99% of all insects, and 100% of all dipterans consumed. Amphipods, leeches, and oligochaetes each composed 1–3% of the diet of males (Table 1). Seeds, tubers, and vegetation composed only small proportions of the diet of male Ruddy Ducks.

Prelaying female Ruddy Ducks consumed 100% invertebrates (Table 1), probably to meet protein demands for oviduct growth and follicle development, as noted in Wood Ducks (*Aix sponsa*) by Drobney (1982). Insects accounted for 84% of all invertebrate foods consumed by

TABLE 1. Proportion (%) of foods in the diet of Ruddy Ducks collected in North Dakota, 1979–1981.

Foods	Males (n = 37)	Females		
		Prelaying (n = 21)	Laying (n = 10)	Postlaying (n = 14)
Invertebrate	91	100	99	73
Macro-				
Insecta	86	84	68	54
Diptera	85 (85)[a]	75 (74)	52 (48)	50 (50)
Trichoptera	1	2	3	2
Odonata		5	2	2
Coleoptera		1	1	
Ephemeroptera		1	9	
Hemiptera			1	
Annelida	4	10	18	
Hirudinea	3	9	12	
Oligochaeta	1	1	6	
Crustacea				
Amphipoda	1			12
Notostraca			1	
Gastropoda			6	
Micro-		6	6	7
Plant	9		1	27
Propagules	5			12
Tubers	3			7
Vegetation	1		1	8

[a] Numbers in parentheses are proportions of the dipteran family Chironomidae in the diet of Ruddy Ducks.

prelaying females. Chironomids were the most important insect family in prelaying female diets. Chironomids constituted 74% of the overall diet and total invertebrates, 88% of all insects, and 99% of all dipterans consumed. Prelaying females consumed a lower proportion of chironomids than males, which resulted in a diet containing a more diverse group of Insecta and other taxa (Table 1). This probably provided sufficient essential amino acids (Krapu and Swanson 1975) required during the prelaying stage, and perhaps maximized efficiency of nutrient utilization (Parrish and Martin 1977).

Laying female Ruddy Ducks continued to use invertebrate foods heavily (Table 1), probably to meet the extremely heavy protein demands of egg production (Robbins 1981). Heavy consumption of protein-rich invertebrates by prelaying and laying female Ruddy Ducks was similar to behavior documented for laying females of other species of ducks (Swanson et al. 1979). Insects were the major dietary component (68% of all foods and 69% of all invertebrates), with Chironomidae being the most important insect family (48% of all foods, 48% of all invertebrates, 71% of all insects, and 92% of all dipterans consumed). Decreased chironomid consumption by laying females resulted in increased dietary diversity among animal foods (Table 1). Increased dietary diversity probably meets the demands of egg production by maintaining a balanced intake of essential amino acids and calcium (Driver et al. 1974).

Postlaying female Ruddy Ducks, like wintering Ruddy Ducks (Barcelona 1976, Hoppe et al. 1986), were more omnivorous. Compared to the diets of prelaying and laying female Ruddy Ducks, the invertebrate component (73%) of postlaying female diets was reduced (Table 1). These data agreed with those of Gray (1980), who indicated that postreproductive females consumed fewer invertebrates than breeding females. Insects composed 54% of all foods and 74% of all invertebrates in the diet of postlaying females. The principal insect family in postlaying female diets was Chironomidae, accounting for 50% of all foods, 68% of all invertebrates, 93% of all insects, and 100% of dipterans. Postlaying females consumed a less diverse array of invertebrate foods than did prelaying or laying females, but the consumption of fruiting bodies (12%, primarily *Chara* oogonia), tubers (7%), and vegetation (8%) increased (Table 1). Thus, postlaying females used seasonally abundant plant foods after the heavy protein demands of the prelaying and laying reproductive stages have ceased. Nevertheless,

muscle replenishment following catabolism (Tome 1984) and feather growth during postbreeding molt continued to require foods rich in amino acids.

REDHEAD FOODS

Redhead foods were determined from 59 adults (21 males, 38 females), of which 52 were collected from Class IV, six from Class III, and one from Class II wetlands. Prairie-nesting Redheads were more omnivorous than Ruddy Ducks. Although invertebrates constituted a smaller part of the Redhead diet compared to that of the Ruddy Duck (Mann-Whitney U-test, $P < 0.0001$), they nevertheless composed 61% of Redhead foods (60% macro-invertebrates and 1% micro-invertebrates). Bartonek and Hickey (1969) also reported substantial use of invertebrates by breeding Redheads. The principal invertebrate class among Redhead foods was Insecta, composing 57% of all foods and 93% of all invertebrates. Chironomidae constituted 53% of the overall diet, 87% of total invertebrates, and 93% of total insects. Fewer invertebrate orders were represented among Redhead foods than in the Ruddy Duck diet (median test, $P < 0.01$). Redheads and Ruddy Ducks did not differ (median test, $P > 0.10$) in the number of insect families occurring in their diets.

Plant matter constituted 39% of Redhead foods. Redheads consumed significantly more (Mann-Whitney U-test, $P < 0.0001$) seeds (25%) than did Ruddy Ducks. *Scirpus* seeds represented the largest percentage (11%) of any plant genus in the Redhead diet. Another 11% of the foods consisted of seeds of emergent plants of temporary (Class II) and seasonal (Class III) wetlands (e.g., *Beckmannia, Alisma, Echinochloa, Eleocharis, Glyceria, Phalaris*), but no genus among this group dominated.

Potamogeton tubers (2%) and vegetation (12%) also were consumed by Redheads. *Potamogeton* and *Zannichellia* were the two most important vascular plant genera in the vegetation portion of the diet. Redheads consumed more vegetation than did Ruddy Ducks (Mann-Whitney U-test, $P < 0.01$), but the two species did not consume different proportions of tubers (median test, $P > 0.10$). More plant families occurred in Redhead (median test, $P < 0.005$) than Ruddy Duck diets.

For cases in which both species were collected from the same wetland ($n = 14$), Redheads were more omnivorous than Ruddy Ducks. In these instances, Redheads consumed fewer invertebrates ($P < 0.01$), more seeds ($P < 0.01$), and more vegetation ($P < 0.01$) (Wilcoxon's signed-rank test) than Ruddy Ducks.

REDHEAD DIETS BY REPRODUCTIVE CATEGORIES

Male and prelaying, laying, and postlaying female Redheads were omnivorous and did not differ among reproductive categories (F-test, df $= 3,55, P > 0.25$) in proportions of invertebrates, seeds, or vegetation in their diets. Male Redheads consumed each of the four main food types: invertebrates (51%), seeds (28%), tubers (3%), and vegetation (18%) (Table 2). The invertebrate component of the diet was considerably larger than Noyes (1983) reported from Nevada. Consumption of invertebrates by breeding males in Manitoba was site-specific (Bailey and Titman 1984; R. O. Bailey, pers. comm.). The most important invertebrate group in the diet of male Redheads was Insecta (Table 2), accounting for 51% of all foods and 100% of invertebrates. The entire invertebrate portion of the male Redhead diet consisted of chironomids, which constituted 51% of the overall diet and 100% of invertebrates, insects, and dipterans. Foremost among plant genera in the "seed" component of male diets were *Scirpus, Alisma,* and *Glyceria* seeds, and *Chara* oogonia (Table 2). Small percentages of several plant genera made up the vegetation portion of the overall male diet (Table 2). Most prominent were *Zannichellia* (5%) and winter buds of *Potamogeton* (5%).

Prelaying, laying, and postlaying females consumed mostly invertebrates in similar proportions (Table 2). Reinecke and Owen (1980) also reported that different reproductive categories of breeding female Black Ducks (*Anas rubripes*) consumed like proportions of invertebrates. In contrast, Noyes (1983) found that laying female Redheads, compared to females in other reproductive classes, consumed significantly more animal than plant matter. In our study, females ate seeds during all reproductive stages (Table 2), as did females of all nonbreeding stages (Bailey and Titman 1984).

Prelaying female Redheads consumed 66% animal matter, 17% seeds, 4% tubers, and 13% vegetation (Table 2). Insecta totaled 83% of all invertebrates in the diet of prelaying females (Table 2). The foremost insect family represented in the foods of prelaying female Redheads was Chi-

TABLE 2. Proportion (%) of foods in the diet of Redheads collected in North Dakota, 1979–1981.

Foods	Males (n = 21)	Females		
		Prelaying (n = 16)	Laying (n = 14)	Postlaying (n = 8)
Invertebrate	51	66	70	63
Macro-				
Insecta	51	55	63	63
Diptera	51 (51)[a]	49 (49)	63 (63)	50 (50)
Trichoptera		5		13
Other		1		
Gastropoda		11	1	
Micro-			6	
Plant	49	34	30	37
Propagules	28	17	28	24
Shallow marsh	10	10	21	
Alisma	5		6	
Beckmannia		2		
Echinochloa			7	
Eleocharis			5	
Glyceria	4	7	1	
Other	1	1	2	
Deep marsh	18	7	7	24
Scirpus	14	7	7	23
Other	4			1
Tubers	3	4	1	
Vegetation	18	13	1	13
Algae	4			1
Chara	1			
Lemna	1		1	
Potamogeton	5			12
Zannichellia	5	6		
Other	2	7		

[a] Numbers in parentheses are proportions of the dipteran family Chironomidae in the diet of Redheads.

ronomidae, which constituted 49% of all foods and 74% of invertebrates, 89% of insects, and 100% of dipterans consumed. The most common plant genera among the seed component were *Glyceria, Beckmannia,* and *Scirpus* (Table 2). Seeds of shallow marsh emergents comprised nearly 60% of all seeds in the diet. Of the identifiable vegetation consumed by prelaying female Redheads, *Zannichellia* (6%) was the primary genus (Table 2).

Laying female Redheads consumed 70% invertebrates, 28% seeds, 1% tubers, and 1% vegetation (Table 2). Insects totaled 63% of all foods and 90% of all invertebrate foods. Chironomidae composed 63% of all foods and 90% of invertebrates, 100% of insects, and 100% of dipterans in the diet of laying females. Most of the seeds were of shallow marsh emergents (primarily *Echinochloa, Alisma,* and *Eleocharis*) and *Scirpus,* and the vegetation consisted of *Lemna* leaflets (Table 2).

Postlaying female Redheads consumed 63% invertebrates, 24% seeds, and 13% vegetation (Table 2). Insecta totaled 63% of all foods and 100% of all invertebrates. Chironomidae was the major family represented, averaging 50% of all foods and 79% of invertebrates, 79% of insects, and 100% of dipterans in the diet. Postlaying females consumed a less diverse invertebrate diet than did prelaying and laying females (Table 2). This might have been because cessation of egg laying lessened requirements for essential amino acids and minerals. Seeds consumed by postlaying females were almost entirely *Scirpus,* and vegetation in the diet was mostly *Potamogeton* winter buds (Table 2). No postlaying birds collected had consumed tubers.

Minor variations in proportions of food types among reproductive classes (Table 2) were less important than the composition of the seed portion of the diet. Whereas virtually all seeds consumed by postlaying females were of deep marsh

plants, over half of the seeds consumed by prelaying and laying female Redheads were of shallow marsh plants (Table 2). Furthermore, the percentage of seeds of shallow marsh species in the diets of prelaying and laying females decreased from 35% in 1979 (a wet year) to <1% in 1980–1981 (dry years). During the wet year of 1979, of the five prelaying and laying female Redheads collected from shallow wetlands, only one had consumed less than 90% seeds of shallow marsh emergents. Two of the four prelaying females and three of the eight laying females collected in 1979 had consumed seeds of shallow marsh emergents in excess of 50%.

DISCUSSION

REDHEADS AND SHALLOW WETLANDS

Our observations indicate that shallow Class II–III marshes, while temporarily containing water in wet years, provide carbohydrate-rich seeds (Sugden 1973, Landers et al. 1977, Reinecke and Owen 1980) for breeding Redheads. Breeding Northern Pintails (*Anas acuta*) (Krapu 1974) and Ring-necked Ducks (*Aythya collaris*) (Hohman 1985) also used shallow wetlands for this purpose.

Use of carbohydrate-rich seed stores in shallow marshes by prelaying and laying female Redheads indicates that they might be using these food resources to meet energy requirements early in the breeding season, when protein-rich invertebrates consumed by Redheads are still rather scarce (Swanson et al. 1974b, Gray 1980). Krapu (1981) suggested that Mallards require a rich energy supply to forage for scarce invertebrates, albeit early-nesting Mallards depended on endogenous fat deposits to meet energy requirements. As a result of their dependence on seeds in shallow marshes as an energy source, Redheads must alter their diet during drought years to accommodate severe reduction in shallow marsh abundance, as Blue-winged Teals (*Anas discors*) were reported to do (Swanson and Meyer 1977). During drought, shallow wetlands and shallow marsh zones of semipermanent (Class IV) wetlands become less available to Redheads. Prelaying and laying females are forced to forage for all their nutrient requirements in the central deep marsh zone of semipermanent wetlands. Consequently, because of a relative lack of availability of seeds of shallow marsh emergents during drought, Redheads consume more seeds of *Scirpus* spp., deep marsh plants.

COMPARISON OF DIETARY STRATEGIES

The reproductive biology of Ruddy Ducks is keyed to their dependence on invertebrate foods in semipermanent wetlands, which they use nearly exclusively. This has been observed on large western marshes (Gray 1980) and the small wetlands of the PPR (Siegfried 1973, Tome 1981, this study). Ruddy Ducks, matched in degree of carnivory among inland diving ducks only by Lesser Scaups, *Aythya affinis* (Rogers and Korschgen 1966, Dirschl 1969, Bartonek and Murdy 1970), might have evolved late initiation of nesting (Hochbaum 1981) because of small body size and storage of only small amounts of endogenous nutrient reserves for reproduction (Tome 1984). By delaying initiation of nesting longer than female Redheads, female Ruddy Ducks can more readily exploit the burgeoning aquatic invertebrate populations (Swanson et al. 1974b, Gray 1980) in deeper, more permanent wetlands. Consequently, prelaying and laying female Ruddy Ducks can obtain nutrient requirements from a diet consisting solely of invertebrates, which are extremely high in energy and protein content (Driver et al. 1974, McCauley and Tsumura 1974).

Whether nesting in large western marshes (Noyes 1983) or in the PPR (this study), Redheads depend on semipermanent wetlands for invertebrate food resources. Unlike Redheads that nest in large and typically isolated western marshes, prairie-nesting Redheads are able to use energy-rich seed stores available in shallow, transient wetlands to fuel foraging for still-scarce invertebrates, which could be one reason why Redheads initiate nesting earlier than Ruddy Ducks (Hochbaum 1981). Redhead dependence on temporary and seasonal wetlands as sources of energy-rich seed stores produces major ramifications for Redhead breeding biology. In contrast to Ruddy Ducks, female Redheads could have difficulty meeting energy demands of foraging for invertebrates during drought years, when shallow wetlands and their seed stores are unavailable. The influence of drought on Redhead foraging upon shallow wetland seed resources and semipermanent wetland invertebrates could create fat and protein shortages for laying females and for males attempting to meet demands placed

on paired birds (Bailey 1985). Redhead dependence on shallow marshes for meeting a major share of energy requirements during breeding could partly explain Redhead migration chronology (Bailey 1985) and the rapid response of Redheads to improved water conditions (Weller 1964).

IMPLICATIONS FOR DIVING DUCK CONSERVATION

Of foremost importance for conservation of these two species is their similar dependence on invertebrates in semipermanent wetlands for the majority of their foods. Males and females of the three reproductive categories of both duck species consumed mostly invertebrates, primarily aquatic insects (Tables 1, 2). Chironomids were the major food regardless of species, sex, or reproductive status. To enhance breeding Ruddy Duck and Redhead populations, productive and diverse aquatic invertebrate communities should be maintained, with emphasis on chironomid populations.

Because of heavy Redhead use of invertebrates in semipermanent wetlands and their opportunistic response to shallow wetlands as temporarily available sources of abundant seed stores, a conservation strategy for breeding Redheads should be developed around the concept of "the prairie wetland complex," as Swanson et al. (1979) proposed for breeding dabbling ducks. Preservation and management of both semipermanent wetlands (providing diverse and productive aquatic invertebrate communities, especially chironomids) and closely associated shallow wetland basins (providing concentrated seed resources in wet years) seem essential to sustain populations of breeding Redheads. To maintain high-quality wetland complexes including shallow and transient (Classes II–III) and more stable, semipermanent (Class IV) wetlands across the Prairie Pothole Region, a serious commitment must be made to preserve and enhance these important habitats.

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