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Title: Diet and Nutrition of Breeding Canvasback and Redhead Ducks at Ruby Lake National Wildlife Refuge, Nevada.

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Diet, nutrition, and foraging strategies of canvasbacks (Aythya valisineria) and redheads (A. americana) were studied by collecting actively feeding birds throughout the reproductive season in 1980 and 1981; samples of available foods were taken each time a bird was collected. Nutrient composition of the aggregate diet was determined for each of 6 reproductive stages (Females, prelaying through brooding; Ducklings, Age Classes I and II). Body composition (lipids and protein) of males and females was determined at each stage of reproduction. Emphasis was placed on the female segment of the redhead and canvasback populations. Canvasback females pursued a conservative foraging strategy, consuming pondweed tubers (84% of diet) prior to laying, but invertebrates (principally caddisfly larvae, dragonfly nymphs, and snails) throughout the remainder of the summer. Preferred food items made up a large part of the diet. With the exception of snails, canvasback females generally did not

consume the most abundant foods available. During the prelaying stage, the diet contained high levels of NFE (nitrogen free extract) (68%), but low levels of protein (17%) and lipids (1.5%). Nutrient content of the diet was constant throughout the remainder of the reproductive season (NFE, 30%; protein, 50%; lipids, 4%). Female canvasbacks had large lipid reserves during prelaying and retained those reserves during laying. However, they used 72% of their lipid reserves during incubation, probably because of high attentiveness to the nest. Redhead females tended to be more opportunistic foragers than canvasbacks. Redheads fed largely on benthic aquatic vegetation (mostly Chara) and seeds except during the laying stage, when invertebrates and bass (Micropterus salmoides) eggs made up the bulk of the diet. The food item composition of the diet varied among all stages and preferred items often were only a small portion of the diet. Nutrient composition of the diet also varied among the reproductive stages and was high in lipids (15%) and protein (50%) only during the laying stage. Energy content of the diet was quite variable (4.4 to 2.4 kcal/g) among the reproductive stages, but was highest during laying. However, female redheads used 34% of their lipid reserves during the laying stage and 56% during the incubation stage. Redheads are parasitic egg layers and apparently devoted much of their energy to locating host

nests and laying large numbers of eggs. Such a strategy requires a high energy, high protein diet, but such foods may be difficult for redheads to obtain. As a result, redheads had reduced energy reserves to expend during incubation and brooding. If redheads had expended energy during incubation at the same rate as canvasbacks, redheads would have depleted their lipid depots 1/2-2/3 of the way through incubation. Thus, these two closely related species pursued quite different reproductive and foraging strategies in the same habitat.

Diet and Nutrition of Breeding Canvasback and Redhead Ducks at Ruby Lake National Wildlife Refuge, Nevada

by

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Personnel at Ruby Lake National Wildlife Refuge

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INTRODUCTION

Food habits and nutrient cycles of breeding waterfowl, principally of dabbling ducks (Anas spp.) (Drobney and Fredrickson 1979; Krapu 1974, 1981; Serie and Swanson 1976; Swanson et al. 1974b) and geese (Ankney and MacInnes 1978; Harwood 1977; Raveling 1979), have received much attention. Generally, lipid reserves are accumulated prior to 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 diving ducks (Aythya spp.), which feed to a greater extent on animal foods throughout the year than do dabblers (Martin et al. 1951), have not been reported.

I investigated the relationship between diet and nutrient cycles of two closely related species of diving ducks, the redhead (Aythya americana) and the canvasback

(A. valisineria). These two species occur together over much of their range and have similar requirements for breeding habitat (Weller 1959). However, they pursue very different nesting strategies; the redhead is parasitic, while the canvasback is not (Weller 1959). Thus their foods and nutrient cycles during the breeding season might be expected to be different, even when they both 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 canvasbacks and redheads; 2) determine the weight and nutrient reserves of the two species during several stages of the breeding cycle; and 3) relate diet and nutrient cycles of the two species to their respective nesting strategies.

STUDY AREA

Ruby Lake National Wildlife Refuge lies in a high mountain valley (1770 m) in northeast Nevada, 80 km southeast of Elko, Nevada. The refuge encompasses approximately 14,980 ha, of which 4,860 ha are wetlands. The study was conducted on a 2,960 ha marsh referred to as the South Sump. Emergent vegetation, mostly hardstem bulrush (Scirpus acutus), comprised approximately 53% of the South Sump; open water comprised 31% and uplands 16% of the South Sump (Bouffard 1981).

Numerous springs at the base of the Ruby Mountains and from within the marsh were the main source of water for the marsh. Because the marsh lies within a hydrologically closed basin and was spring-fed, water levels tended to be relatively constant both within and between years. The most recent reduction of water levels in the South Sump occurred in 1961. In 1980-81, average water depth for most of the South Sump was approximately 1.5 m, with depths of 3-4 m occurring in several of the large, open water areas. Canvasbacks and redheads seldom foraged in these large, deep areas. The marsh supported a high density of largemouth bass (Micropterus salmoides) and a low density of several species of trout (Salmo spp.). Aquatic invertebrates were the primary food for both bass and trout (Carmichael, unpubl. data).

Most breeding canvasbacks and redheads at Ruby Lake NWR nest in the South Sump (Bouffard 1981).

METHODS

Ducks were collected by shooting during spring and summer 1980 and 1981. All birds were observed feeding for a minimum of 15 minutes prior to collection (Swanson and Bartonek 1970). Immediately after collection, esophageal contents were removed and preserved in 75% ethanol.

Classification of reproductive status of females was primarily based on ovarian condition (Krapu 1974). Females were assigned prelaying status from arrival to initiation of egg laying. Laying females were those that had at least one ruptured follicle, and either an egg in the oviduct or the presence of enlarged unruptured follicles. Incubating females possessed incubation patches and regressed ruptured follicles. Brooding females were observed with a brood. Reproductive status of paired males was based on association with a female of known reproductive status. Age classes of ducklings were determined by the classification of Gollop and Marshall (1954).

Foods consumed were expressed as percent occurrence and as aggregate percent by weight (Swanson et al. 1974a). Most food items were dried at 65° C for 24 hours; tubers and seeds were dried at 65° C until constant weight was obtained. Dry weight was used as the measure of food quantity because dry weight reflected nutritional content and avoided biases caused by variable water content of

food items (Reinecke and Owen 1980). Only birds with food in the esophagus were used for diet analyses; adult birds with little (less than 0.05 g) or no food in the esophagus were included in analyses of lipid and protein reserves only.

Measurements of availability of food in the environment were taken at the site and time of collection of each bird. During the prelaying period, when birds foraged in open water areas, a column sampler was used to sample a benthic area of approximately 45 cm^2 (Swanson 1978). As birds shifted to foraging areas within and along emergent vegetation, 3- 1 m net sweeps (1mm mesh) covering an area of approximately 1.5 m^2 were used to sample benthic and pelagic organisms. Samples of food availability for all birds beyond the prelaying stage were obtained with net sweeps. Samples were preserved in 10% Formalin and returned to the laboratory for processing.

Preference (selectivity) for food items was calculated using a relative preference ranking technique (Johnson 1980). The order of preference rankings of food items was based on the difference between the rank of food item usage and availability; those food items with the greatest difference were given the highest relative preference ranking. Without entering into a discussion on the theoretical differences between the terms preference and selectivity as discussed by several authors (Ellis et

al. 1976, Pirnie 1935), the term preference as described by Johnson (1980) was used to specify differences between food usage and food availability. Johnson (1980) defined preference as a reflection of the likelihood of a particular item being chosen if offered on an equal basis with others. Only those food items that occurred in the esophagus of at least one bird were considered as potential food and included in the food preference analyses. Portions of some food items in the samples of available foods were either undigestible or not utilized and dry weights were corrected to reflect utilized portions. Fifty percent of the weight of muskgrass (Chara spp.) taken in samples was considered as available food; approximately 50% of muskgrass was roots and main branches, neither of which were observed in the esophagi of ducks that fed on muskgrass. Snail shells and cases of caddisfly larvae provide waterfowl with certain minerals, but contain little nutritional value relative to their weight. Therefore, weights of caddisfly larvae in cases was multiplied by 0.356 and weights of snails by 0.30 to account for the weights of cases and shells, respectively. Values for nutritional content (lipids, protein, nitrogen free extract (NFE) and fiber) of most food items were obtained from published sources (Anderson and Low 1976, Krapu and Swanson 1975, Gortner 1934, Reinecke and Owen 1980, Sugden 1973). The protein content of bass eggs was determined by the micro-Kjeldahl procedure at the Oregon

State University Horticultural Laboratory. Nutrient content of the composite diet of canvasbacks and redheads was calculated by combining proximate analyses data and aggregate dry weight data (Reinecke and Owen 1980). Caloric content of the diet (energy) of canvasbacks and redheads was calculated by multiplying the metabolizable energy value of each nutrient (Sturkie 1965:242) times the proportion of the nutrient in the composite diet and summing the products; energetic content of the diet was expressed as kcal per g of food.

Lipid and protein content of ducks were determined by standard procedures (Horowitz 1970) and by the Kjeldahl nitrogen technique, respectively, after plucking and grinding of carcasses (Brisbin 1968).

Prior to statistical analyses, percentages were transformed (arcsin $\sqrt{x}$) to improve normality (Zar 1974). One-way analyses of variance were used to compare foods consumed by ducks among all reproductive stages; differences in mean lipid reserves, protein reserves, body weights, and organ weights were compared with a t-test. Adult and yearling birds were combined in the analyses because body weights were not significantly different (Canvasbacks, $t=0.20$, 49df, $P>0.05$; Redheads, $t=0.81$, 49df, $P>0.05$). The diets of males during the prelaying and laying stages were the same (Canvasbacks, $t=0.55$, 6df, $P>0.05$; Redheads, $t=2.24$, 7df, $P>0.05$), and these reproductive stages were merged to provide larger sample sizes when testing for differences in diets between sexes.

RESULTS

Sample sizes were small and collection of specimens was constrained by several factors. The large expanse of the marsh and restricted mobility within the marsh made collection of specimens difficult and time consuming. However, the distribution and number of duck collections throughout the marsh was approximately proportionate to the distribution of ducks within the marsh. The size of the breeding populations also limited the size of the samples. The combined collections in 1980-81 represented 5.0% and 3.5% of the female segment of the estimated breeding populations (Bouffard 1980, 1981) of redheads and canvasbacks, respectively. The small samples restricted analysis of data and interpretation of results. Despite these constraints and limitations, several obvious differences in diet and nutrient reserves of canvasbacks and redheads were apparent, especially among females.

Canvasbacks

Ninety-six canvasbacks were collected during 1980 and 1981 (15 males, 51 females, 30 ducklings). During the prelaying stage, 6 males and 15 females with food in the esophagus were collected; during the laying stage, 2 males and 6 females contained food. Twelve incubating females, 7 brooding females, and 30 ducklings were included in the diet analyses.

Diet of Paired Males and Females.--Esophageal contents of 8 paired males (6 during the prelaying and 2 during the laying stage of their mates) and 15 paired prelaying females were not significantly different ($P>0.05$) in the proportion of plant and animal foods they contained (Table 1). The diet of males consisted of about 90% plant and 10% animal matter. Tubers of pondweed (primarily Potamogeton pectinatus) were the dominant food item of males and comprised about 80% of the aggregate diet. Tubers were consumed by 88% of canvasback males. The invertebrate portion of the diet was almost exclusively snails and constituted about 10% of the aggregate diet. Females during the laying stage consumed a much greater proportion of invertebrates (77.7%) than did paired males (10.2%) ($P<0.05$).

Diet of Breeding Females.--Esophageal contents of prelaying females contained 92.5% plant food and 7.5% animal matter. Tubers of pondweed accounted for nearly all of the plant foods consumed (91%) and amounted to 84% of the aggregate diet. Tubers were probably selected because of their high energy content (74% NFE; Anderson and Low 1976). Dragonfly nymphs (Anisoptera:Aeshnidae and Libellulidae) and snails (Gastropoda:primarily Lymnaeidae and Physidae) contributed 91% to the invertebrate portion of the diet and 6.8% to the aggregate diet.

During the laying stage, females consumed significantly more ($P<0.05$) invertebrates (77.7%) than

Table 1. Esophageal contents of breeding canvasbacks, Ruby Lake National Wildlife Refuge, Nevada, 1980-81.

	% Occurrence					Aggregate % Weight				
	Males	Females				Males	Females			
Food Item	(8)[a]	P[b] (15)	L (6)	I (12)	B (7)	(8)	P (15)	L (6)	I (12)	B (7)
ANIMAL										
Insecta	13	27	100	83	100	tr[c]	4.7	51.4	44.0	69.6
Odonata		20	83	75	71		4.0	11.5	23.6	25.2
Anisoptera		13	67	75	57		3.9	10.0	21.8	24.3
Aeshnidae		7	50	75	57		3.3	2.7	17.3	24.3
Libellulidae		13	50	42			0.6	7.3	4.5	
Zygoptera		20	67	50	29		0.1	1.5	1.8	0.9
Coenagrionidae		20	67	50	29		0.1	1.5	1.8	0.9
Trichoptera		13	67	67	57		0.4	32.1	18.9	38.7
Limnephilidae		13	67	58	57		0.4	32.1	18.8	38.7
Other				8					0.1	
Diptera		20	67	50	14		0.3	7.7	1.4	5.7
Chironomidae		20	67	50	14		0.3	7.5	1.0	4.3
Tabanidae			33	8	14			0.2	0.3	1.3
Other			17	17	14			tr	0.1	0.1
Coleoptera			17					0.1		
Ephemeroptera	13	7	17	17		tr	tr	tr	0.1	
Mollusca	25	27	67	67	71	10.2	2.9	26.2	33.8	18.6
Gastropoda	25	27	67	67	71	10.2	2.9	26.2	33.8	18.6
Lymnaeidae and Physidae	25	13	67	58	71	10.2	2.7	26.2	33.7	18.6
Planorbidae	13	20		33	14	tr	0.2		0.1	tr
Other			17	8	14			0.1	tr	tr
TOTAL Animal Matter	38	40	100	83	100	10.2	7.6	77.7	77.8	88.2
PLANT										
Vegetation	88	93	50	58	14	80.3	90.3	20.6	21.2	0.6
Potamogeton (tubers)	88	87	17	50		80.3	84.0	16.2	21.1	
Chara sp.		7		17			1.0		0.1	
Phycomycete fungus		7					5.1			
Unidentified		13	33		14		0.2	4.4		0.6
Seeds	100	73	67	42	57	9.5	2.1	1.7	1.0	11.2
Potamogeton sp.	75	60	33	17	29	5.4	1.7	0.7	0.4	1.2
Scirpus sp.	75	40	67	42	29	4.1	0.4	1.0	0.4	10.0
Other seeds		7		8			tr		0.2	
TOTAL Plant Matter	100	100	67	67	57	89.8	92.4	22.3	22.2	11.8

[a]Sample size.

[b]P = Prelaying, L = Laying, I = Incubating, B = Brooding

[c]Trace (less than 0.1%)

during the prelaying stage (7.5%) (Table 1). Caddisfly larvae (Trichoptera:Limnephilidae), snails, and dragonfly nymphs combined, made up 88% of the invertebrates consumed. Although midge larvae (Diptera:Chironomidae) and damselfly nymphs (Zygoptera:Coenagrionidae) were important on an occurrence basis (both 67%), they contributed only 9% total to the diet by weight.

Esophageal contents of laying, incubating, and brooding females were not significantly different ($P>0.05$) in the proportion of plant and animal food. Consumption of invertebrates by canvasback females remained high during the incubation period, accounting for 77.8% of the diet. Snails, dragonfly nymphs, and caddisfly larvae were the primary animal foods in the diet (74.5%). Dragonfly nymphs increased to over twice the proportion (21.8%) found in the diet of laying females (10.0%) and caddisfly larvae decreased by approximately the same amount. Tubers of pondweed represented 21% of the aggregate diet and were consumed by 50% of incubating females.

Brooding females consumed a diet consisting of 88.1% animal food. The principal invertebrates in the diet in decreasing order of biomass were caddisfly larvae, dragonfly nymphs, and snails; these 3 food items comprised 93% of the animal food consumed by brooding females. The most frequently consumed foods were dragonfly nymphs and snails.

Diet of Canvasback Ducklings.--Animal food comprised 85.4% and 89.8% of the diet of Class I and Class II ducklings, respectively (Table 2). Snails, caddisfly larvae, and damselfly nymphs contributed 92% to the invertebrate portion of the diet of Class I ducklings. The diet of Class II ducklings was likewise largely composed of snails and caddisfly larvae; midge larvae also were an important food item. Midges accounted for over 9% of the aggregate diet of Class II ducklings as a result of heavy use by 2 ducklings collected at one location at night. Seeds (primarily Scirpus acutus) comprised the majority of plant matter (95% and 99%) in the diet of both Class I and Class II ducklings.

Food Preference.--Dragonfly nymphs and caddisfly larvae were the 2 most preferred foods of female canvasbacks in each of the reproductive stages where preference rankings were calculated (Table 3). Relative preference rankings could not be calculated for laying females because of small sample sizes. Relatively low preference for snails was apparent during all reproductive stages. Snails were the most abundant animal food in the environment, especially after early spring. Tubers of pondweed were the most preferred food item for males during the prelaying stage.

Caddisfly larvae were a highly preferred food item by both Class I and Class II ducklings. Snails had a low preference ranking as food of canvasback ducklings of all

Table 2. Esophageal contents of canvasback and redhead ducklings, Ruby Lake National Wildlife Refuge, Nevada, 1980-81.

	% Occurrence				Aggregate % Weight			
	Canvasback		Redhead		Canvasback		Redhead	
Food Item	I[a] (12)[b]	II(18)	I (11)	II (16)	I (12)	II (18)	I (11)	II (16)
ANIMAL								
Insecta	83	78	82	44	46.5	43.2	41.6	2.0
Odonata	58	11	18		20.3	1.3	7.0	tr[c]
Zygoptera	58	11	18		20.3	1.3	7.0	tr
Coenagrionidae	58	11	18		20.3	1.3	7.0	tr
Trichoptera	33	56			20.5	32.5		
Limnephilidae	33	50			20.3	32.4		
Other	8	6			0.2	0.1		
Diptera	42	33	55	25	1.7	9.3	12.7	0.6
Chironomidae	42	33	55	25	1.7	9.3	12.7	0.6
Coleoptera	25			6	4.0			0.1
Ephemeroptera		11	18			0.1	3.0	
Hemiptera			46	25			18.9	1.3
Corixidae			46	25			18.9	1.3
Crustacea		6	9			tr	1.8	
Amphipoda		6	9			tr	1.8	
Talitridae		6	9			tr	1.8	
Mollusca	83	67	9		37.7	46.4	3.8	
Gastropoda	83	67	9		37.7	46.4	3.8	
Lymnaeidae and Physidae	83	67	9		37.7	46.4	3.8	
Other	33	11	9	6	1.2	0.2	tr	0.1
TOTAL Animal Matter	100	100	82	44	85.4	89.8	47.2	2.1
PLANT								
Vegetation	8	11	55	100	0.8	tr	36.9	92.4
Potamogeton sp. (tubers)		6		6		tr		0.6
Chara sp.			55	88			36.9	79.3
Zannichellia sp.				13				12.5
Unidentified	8	6			0.8	tr		
Seeds	42	44	36	31	13.8	10.2	15.9	5.5
Potamogeton sp.	25	6	18	6	1.8	0.1	2.1	0.4
Scirpus sp.	33	39	27	25	9.8	10.1	13.3	5.1
Other seeds	8		9		2.2		0.5	
TOTAL Plant Matter	42	55	82	100	14.6	10.2	52.8	97.9

[a]I = Age Class I, II = Age Class II

[b]Sample size.

[c]Trace (less than 0.1%)

Table 3. Relative preference ranking for food items by breeding canvasbacks and redheads, Ruby Lake National Wildlife Refuge, Nevada, 1980-81 (1 = most preferred, 10 = least preferred).

	Canvasbacks						Redheads		
	Females			Males	Ducklings		Females		Ducklings
Food item	Prelaying	Incubating	Brooding	Prelaying	Age Class I	Age Class II	Prelaying	Laying	Age Class I
Caddisfly larvae	1	1	2		2	1	1	2	
Dragonfly nymphs	2	2	1				4	3	
Pondweed (tubers)	3	3		1					
Mayfly larvae	4	6				2	6		
Phycomycete fungus	5						3		
Rooted vegetation (Chara, Zannichellia, Potamogeton)	6	4					8	8	6
Damselfly nymphs	7	7			3	6	10	4	5
Snails	8	5	5	2	5	5	9	9	1
Seeds	9	9	4	3	4	4	7	7	3
Midge larvae	10	8	3			3	5	6	4
Beetles					1		2	5	
Water boatmen									2
Bass eggs								1	

ages.

Body Weight.--A slight, but non-significant ($P>0.05$), increase in body weight of females occurred from prelaying ($\bar{X}$=1219 g) to the laying stage ($\bar{X}$=1255 g). A significant loss ($P<0.05$) of body weight occurred from laying through incubation. Lipid levels and body weight were highly correlated (r=0.89) and decreased body weight was principally a result of utilized lipid reserves. Females lost 339 g (27%) of body weight from peak weight at laying to the low at brooding.

No significant change ($P>0.05$) in body weights of males occurred from the prelaying stage (1319 g, N=8) to the laying stage (1248 g, N=4) of their mates.

Body Components.--Lipid content was determined for 43 female and 12 male canvasbacks (Tables 4,5). Mean lipid levels of females did not change from prelaying (459 g) to laying (457 g); however, a significant decline ($P<0.05$) occurred during incubation and represented a 72% loss in lipid reserves from the peak at prelaying. Brooding females contained an average of 45 g of lipids, which represented a loss of 65% from the incubation stage and a total reduction of 90% from the prelaying stage. Mean lipid levels of males decreased 98 g (19%) from the prelaying to the laying stage, but the loss was not significant (t=0.97, 10df, $P>0.05$).

Protein content of 24 females reached a peak of 226 g

Table 4. Changes in body weight, lipids, and protein of female canvasbacks by reproductive stage, Ruby Lake National Wildlife Refuge, Nevada, 1980-81. Sample sizes are in parentheses.

	Prelaying		Laying			Incubating			Brooding	
Weight (g)	(mean ± SE)	P[a]	(mean ± SE)	% change[b]	P	(mean ± SE)	% change	P	(mean ± SE)	% change
Body	1219 ± 26 (17)	NS	1255 ± 32 (6)	+3	***	1016 ± 31 (12)	-19	*	916 ± 32 (8)	-10
Lipids	459 ± 48 (18)	NS	457 ± 54 (6)	-0.4	***	127 ± 24 (12)	-72	*	45 ± 10 (7)	-65
Protein	220 ± 4 (6)	NS	226 ± 5 (6)	+3	*	199 ± 7 (10)	-12	NS	178 ± 7 (4)	-11

[a] Significance level of t-test between means in adjacent columns. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS represents $P > 0.05$.

[b] Percent change from preceding reproductive stage.

Table 5. Changes in body weight and lipids of male canvasbacks and redheads by reproductive stage, Ruby Lake National Wildlife Refuge, 1980-81. Sample sizes are in parentheses.

	CANVASBACKS			REDHEADS		
	Prelaying		Laying	Prelaying		Laying
Weight (g)	(mean ± SE)	P[a]	(mean ± SE)	(mean ± SE)	P	(mean ± SE)
Body	1319 ± 32 (8)	NS	1248 ± 40 (4)	1063 ± 33 (8)	NS	1014 ± 43 (5)
Lipids	519 ± 55 (8)	NS	421 ± 93 (4)	305 ± 69 (8)	NS	239 ± 48 (4)

[a] Significance level of t-test between means in adjacent columns. * = $P < 0.05$; ** = $P < 0.01$; NS represents $P > 0.05$.

during laying and a low of 178 g during brooding, a 21% loss (Table 4). Incubating females possessed an average of 199 g of protein, a loss of 27 g from levels during the laying period. Canvasback eggs contained 46.1% protein. The average weight of canvasback eggs (67.5 g, Bouffard 1981), the protein content of the eggs (46.1%), and the average clutch size (7.3 eggs, Bouffard 1981) were used to derive a minimal estimate of 227 g of protein required by females to produce a clutch of eggs. Protein content of females during laying decreased only 27 g; apparently most protein required for production of eggs was obtained from food, as was reported for female mallards (Krapu 1981).

Redheads

Ninety-six redheads were collected during 1980 and 1981 (17 males, 51 females, 28 ducklings). Six of the males collected during the prelaying period and 3 collected during the laying stage contained food in the esophagus. Thirteen prelaying females, 11 laying females, 6 incubating females, 7 brooding females, and 27 ducklings were included in the diet analyses.

Diet of Paired Males and Females.--No significant difference ($P>0.05$) was found in the diet of 9 males and 13 prelaying females. Males consumed a diet consisting of 64.9% vegetation, 15.6% seeds, and 19.5% animal matter (Table 6). Bulrush seeds and muskgrass represented most of the plant foods consumed. Eleven percent of the males

Table 6. Esophageal contents of breeding redheads, Ruby Lake National Wildlife Refuge, Nevada, 1980-81.

	% Occurence					Aggregate % Weight				
	Males	Females				Males	Females			
Food Item	(9)[a]	P[b] (13)	L (11)	I (6)	B (7)	(9)	P (13)	L (11)	I (6)	B (7)
ANIMAL										
Insecta	44	77	100	100	14	7.5	22.1	40.4	15.2	0.2
Odonata	11	38	64	33		1.9	4.0	21.5	0.8	
Anisoptera	11	8	27	17		1.2	0.5	15.7	0.2	
Aeshnidae	11		27	17		1.2		15.1	0.2	
Libellulidae		8	18				0.5	0.6		
Zygoptera	22	38	55	33		0.7	3.5	5.8	0.6	
Coenagrionidae	22	38	55	33		0.7	3.5	5.8	0.6	
Tricnoptera	22	23	46	50		4.9	6.9	4.4	1.2	
Limnephilidae	22	23	46	50		3.2	6.9	4.0	1.1	
Other	11		9	17		1.7		0.4	0.1	
Diptera	22	46	91	83	14	0.3	7.0	12.5	13.2	tr[c]
Chironomidae	22	46	73	67	14	0.3	7.0	12.2	13.2	tr
Other			27	17				0.3	tr	
Coleoptera		15	9				0.3	1.9		
Ephemeroptera	22	8	18	17		0.4	3.9	0.1	tr	
Hemiptera					14					0.2
Corixidae					14					0.2
Mollusca	22	54	46	67		0.2	1.4	0.3	17.4	
Gastropoda	22	54	46	67		0.2	1.4	0.3	17.4	
Lymnaeidae and Physidae	22	31	27	67		0.2	0.6	0.2	16.4	
Planorbidae	11	46	46	67			0.8	0.1	1.0	
Crustacea	11	23	18			0.4	1.1	tr		
Amphipoda	11	23	18			0.4	1.1	tr		
Talitridae	11	23	18			0.4	1.1	tr		
Bass Eggs	11		36	17		11.1		34.3	15.9	
Other	11		36	33	29	0.3		1.8	0.1	0.4
TOTAL Animal Matter	67	92	100	100	43	19.5	24.6	76.8	48.6	0.6
PLANT										
Vegetation	78	77	64	50	100	64.9	67.0	13.4	16.5	99.3
Chara sp.	67	77	46	50	100	62.8	59.0	10.6	16.5	99.3
Phycomycete fungus	11	23				1.7	8.0			
Unidentified	11		18			0.4		2.8		
Seeds	44	77	91	100	43	15.6	8.4	9.8	34.9	0.1
Potamogeton sp.	33	8	27	17		5.4	0.7	0.5	tr	
Scirpus sp.	33	77	91	100	43	10.2	7.7	9.3	34.9	0.1
Other seeds		8	9					tr		
TOTAL Plant Matter	89	100	91	100	100	80.5	75.4	23.2	51.4	99.4

[a]Sample size.

[b]P = Prelaying, L = Laying, I = Incubating, B = Brooding

[c]Trace (less than 0.1%)

and 23% of the prelaying female redheads consumed small amounts of phycomycete fungus attached to muskgrass. Males consumed significantly less ($P>0.05$) invertebrates than laying females (19.5% and 76.8%, respectively)

Diet of Breeding Females.--Three-fourths of the diet (by weight) of prelaying females was comprised of plant food, 78% of which was muskgrass. Midge larvae, caddisfly larvae, and mayfly nymphs (Ephemeroptera:Baetidae and Caenidae) collectively accounted for 17.8% of the aggregate diet.

During the laying stage, females consumed a significantly higher ($P<0.05$) amount of animal matter than did males or prelaying females. Animal food, 45% of which was bass eggs, comprised 76.8% of the diet of laying females. Bass eggs were a rich source of protein (63.9%), were consumed by 36% of the laying females, and comprised 34% of their aggregate diet. Consumption of fish eggs by breeding waterfowl in freshwater marshes has not been previously reported. Utilization of herring (Clupea harengus) eggs along the Pacific Coast was reported by Munro (1941) for Greater scaup (Aythya marila) and by Bayer (1980) for several species of diving ducks (Aythya spp.), including canvasbacks and redheads. Other animal foods frequently consumed by laying female redheads were dragonfly nymphs, midge larvae, and damselfly nymphs (collectively 34% of the diet). Muskgrass contributed

10.6% and bulrush seeds 9.3% to the diet.

Animal matter decreased in prominence in the diet of incubating female redheads and represented 48.6% of the aggregate diet. Ranked by order of decreasing amount consumed, snails, bass eggs, and midge larvae combined for most of the animal food consumed (96%). Bulrush seeds were found in all incubating females and amounted to 34.9% of the diet. One incubating female had over 14 grams of bulrush seeds in the esophagus when collected. Bulrush seeds have a high energy content (66% NFE) and consumption of seeds may reflect the high energy demand of incubating redheads. Krapu (1974a:288) stated "while egg-producing hens are in need of a high protein diet, postlaying hens are primarily in need of high energy foods to maintain body functions".

The diet of brooding females was nearly exclusively vegetation and consisted of 99.3% muskgrass. Abundance and variety of invertebrates were relatively low in most ponds selected as brood rearing areas (Table 7) relative to canvasback brood areas. Most redhead broods occurred in landlocked ponds isolated from the main body of the marsh. These areas supported extensive growths of muskgrass; muskgrass comprised over 90% of the foods available to brooding female redheads.

Diet of Redhead Ducklings.--The diet of redhead ducklings reflected the low abundance and variety of invertebrates in redhead brood rearing ponds relative to

Table 7. Number of taxa and mean weight of invertebrates sampled at sites where brooding and duckling canvasbacks and redheads were collected, Ruby Lake National Wildlife Refuge, Nevada, 1980-81. Sample sizes are in parentheses.

Collection Site	Taxa per sample (mean ± SE)	Weight (g) (mean ± SE)
Brooding redheads (7)	3.86 ± 0.55	0.11 ± 0.03
Redhead ducklings (14)	3.36 ± 0.33	0.08 ± 0.02
Brooding canvasbacks (7)	5.60 ± 0.53	0.37 ± 0.08
Canvasback ducklings (24)	5.04 ± 0.29	0.29 ± 0.05

the rest of the marsh. Water boatmen (Corixidae) were common in these brood rearing areas and comprised the majority of the invertebrate portion of the diet of redhead ducklings, especially during the Class I stage (Table 2). Although 82% of Class I ducklings consumed invertebrates, less than one-half of the diet by weight (47.2 %) consisted of animal matter. Muskgrass contributed 36.9% to the aggregate diet of Class I redheads; seeds, primarily bulrush seeds, amounted to 15.9% of the diet.

Redhead ducklings during the Class II stage drastically decreased their consumption of invertebrates (2.1% of the diet; Table 2). Muskgrass comprised 79.3% and horned pondweed (Zannichellia palustris) 12.5% of the foods consumed. Plant matter accounted for 97.9% of the diet.

Food Preference.--Caddisfly larvae were the most preferred food item of prelaying redhead females (Table 3). In decreasing order of preference, bass eggs, caddisfly larvae, and dragonfly nymphs were the preferred food items of laying females. A high degree of selection was indicated by those birds that foraged on bass eggs; bass eggs comprised 94% of all foods consumed by 4 laying female redheads. Field observations further indicated a high degree of selectivity for bass eggs by redheads. Redhead pairs appeared to search for bass nests along the

edge of bulrush. On 2 separate occasions I observed what I believe was an interaction with the male bass guarding the nest. The male redhead repeatedly made short duration dives, each time surfacing in an aggressive posture; each dive was followed by the female diving at the same location. After collection, the esophagi of the paired birds were examined and the females' contained bass eggs. One male redhead consumed a small amount of bass eggs. Age Class I ducklings preferred snails and water boatmen. Snails were relatively scarce in the ponds where redhead broods were typically found (5.4% of food available compared to 51.5% in areas frequented by Class I canvasbacks), yet composed 3.8% of the diet of Class I ducklings. Water boatmen comprised 18.9% of the diet. Relative preference rankings could not be calculated for redhead males, incubating females, brooding females, and Class II ducklings because of small sample sizes and a low variety of food items in the diet. During the incubating and brooding stages, most of the diet of female redheads was composed of abundant food items. Bulrush seeds and snails were abundant foods during incubation, and muskgrass was abundant during both incubation and brooding. Because preference is usually indicated for foods that are not abundant, these items would probably have low preference rankings.

Body Weight.--Weights of prelaying and laying females were nearly identical ($\bar{x}$=1062 g and 1060 g, respectively)

(Table 8). Females experienced a significant decline ($P<0.05$) in body weight from laying through incubation. Total weight loss from prelaying to the brooding period was 231 g or 22% of maximum weight attained.

Male redheads lost an average of 49 g of body weight from the prelaying stage to the laying stage of their mates. More definitive patterns of weight changes in male redheads may be obscured by the small sample sizes.

Body Components.--Lipid reserves of female redheads reached a maximum level during prelaying (201 g, Table 8). Lipids decreased significantly during both the laying and incubation periods ($P<0.05$). A further decrease occurred during brooding, when a minimum level of 71 g was reached. Lipid reserves during the brooding period were only 17% of prelaying levels. Lipid reserves of redhead males declined an average of 66 g (22%) from the prelaying stage to the laying stage; this was not a significant change ($t=0.63$, 10df, $P>0.05$).

Changes in protein content of 30 female redheads closely paralleled the pattern in canvasbacks, a 22% loss from a high of 201 g at laying to a low of 156 g during brooding.

Table 8. Changes in body weight, lipids, and protein of female redheads by reproductive stage, Ruby Lake National Wildlife Refuge, 1980-81. Sample sizes are in parentheses.

	Prelaying		Laying			Incubating			Brooding	
Weight (g)	(mean ± SE)	P[a]	(mean ± SE)	% change[b]	P	(mean ± SE)	% change	P	(mean ± SE)	% change
Body	1062 ± 22 (15)	NS	1060 ± 22 (14)	-0.2	***	913 ± 22 (8)	-14	*	831 ± 21 (8)	-9
Lipids	419 ± 31 (15)	**	277 ± 24 (14)	-34	***	123 ± 23 (8)	-56	NS	71 ± 17 (8)	-42
Protein	186 ± 9 (6)	NS	201 ± 4 (13)	+8	**	179 ± 5 (7)	-11	*	156 ± 8 (4)	-13

[a] Significance level of t-test between means in adjacent columns. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS represents $P > 0.05$.

[b] Percent change from preceding reproductive stage.

DISCUSSION

Foraging Strategy

Female canvasbacks and redheads at Ruby Lake NWR appeared to pursue different foraging strategies and undergo different patterns of lipid utilization. These differences appear to be related to differences in the reproductive strategies of the two species.

Canvasbacks and redheads both shifted from plant foods during the prelaying period to animal foods during laying. An increase in invertebrate consumption by female ducks during the breeding season is a response to the increased protein and nutrient demands associated with egg production (Krapu 1974). Whereas canvasbacks maintained a high proportion of animal food in the diet throughout the breeding season, redheads reverted to a diet of plant foods after laying.

Redheads appear to be more opportunistic feeders than canvasbacks. The diet of redheads changed among the reproductive stages and, except during laying, redheads consumed the most abundant food items available. During the laying stage, the protein requirements of egg production possibly necessitated that redheads seek less abundant animal foods capable of satisfying those requirements. Other than during the laying period, preferred food items often did not make a large contribution to the diet of redheads.

Contrary to the opportunistic foraging behavior of redheads, the diet of canvasbacks was generally dominated by a few major items and the composition of the diet remained relatively constant during all reproductive stages after prelaying, including the duckling stage. Preferred food items made up most of the diet of canvasbacks; canvasbacks generally did not consume the most abundant foods available. The lone exception was the frequent consumption of snails, which were previously reported as an important food of reproducing canvasbacks (Bartonek and Hickey 1969).

Body Components

Body components presumably reflect the condition of the ducks during the approximate mid-points of the several stages of the reproductive cycle. However, body reserves, especially lipids, change dynamically during the stages. My measures of the body components are an index to the condition of the ducks and do not measure absolute maximum or minimum levels during each stage. Likewise, changes from one stage to the next are indexes to the actual changes that occurred.

The pattern of protein deposition and utilization was similar in canvasbacks and redheads (Fig. 1). Both species displayed a slight increase in body protein levels from prelaying to laying and a steady loss through

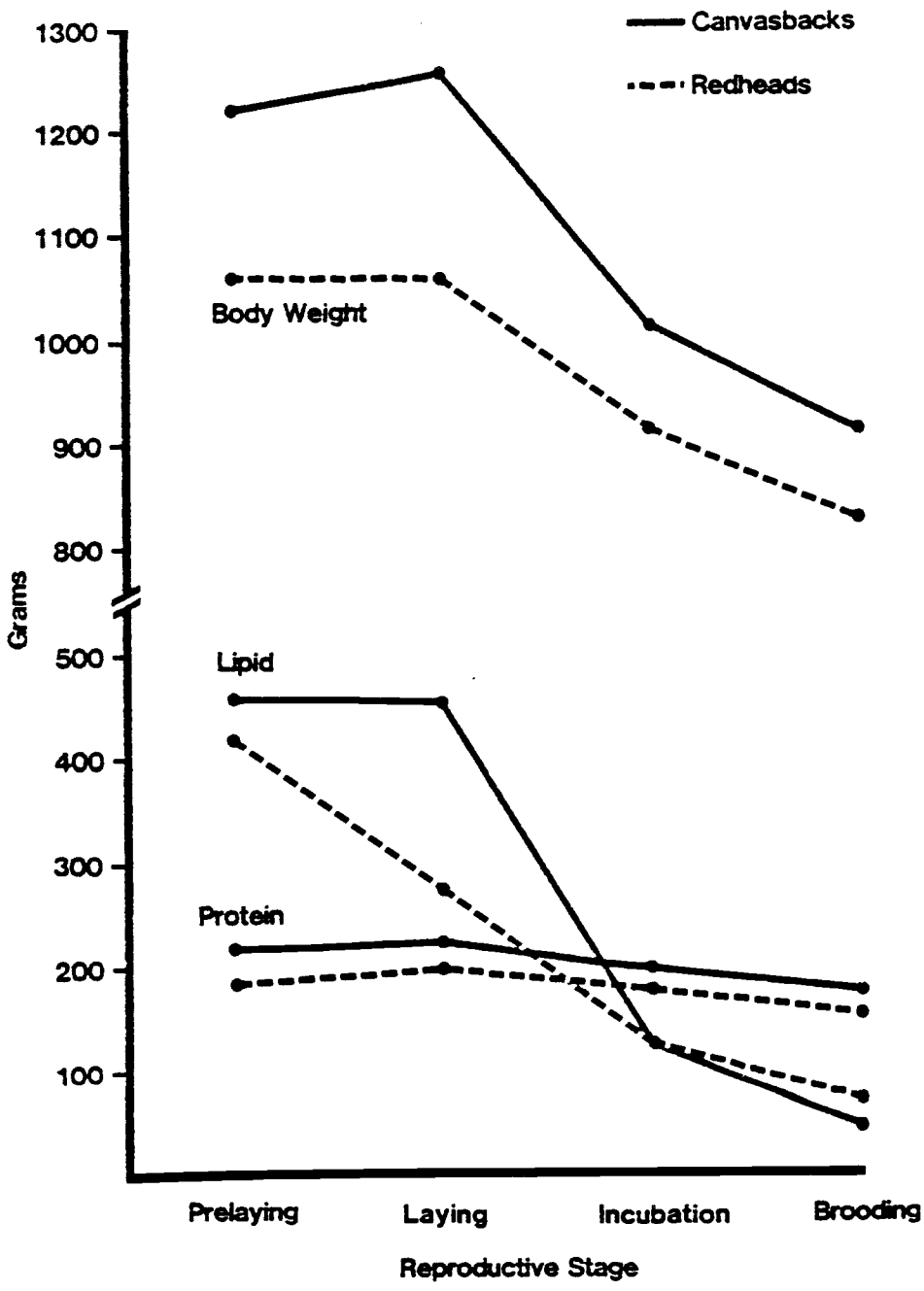

Fig. 1. Body weight, lipid reserves, and protein reserves of female canvasbacks and redheads during the reproductive season, Ruby Lake National Wildlife Refuge, 1980-81.

brooding. The dynamics of lipid reserves, however, were quite different between the two species and may reflect dissimilar reproductive strategies. Canvasbacks preserved their lipid reserves during laying and expended them during incubation. Presumably energy and nutrients required for egg production were met by the foods consumed. The loss of lipid reserves during incubation probably resulted from restricted feeding and high attentiveness to the nest. Redheads, however, used much of their lipid reserves during laying and continued to use lipid reserves at a constant rate during incubation. During incubation, redheads could not use their lipid reserves at the same rate as canvasbacks without exhausting all body lipids. Hence, redheads are probably less attentive to nests than canvasbacks.

The loss of lipids by redheads during laying (34% loss) probably resulted from the energetic cost of parasitic egg laying. Approximately two-thirds (65%) of canvasback nests were parasitized by redheads (Bouffard 1981). Based on the average redhead clutch size (8.3 eggs) and the average number of parasitic eggs laid (3.5 eggs), redheads laid 1.6 times as many eggs as canvasbacks (Bouffard 1981). Beyond the energy content of additional eggs, redheads must utilize energy in locating hosts' nests. Consequently, redheads devoted a much larger amount of lipids to laying but much less to incubation and brooding than did canvasbacks.

Nutrient Composition of the Diet

The nutrient content of the diet of canvasbacks was constant from laying through brooding (<5% lipid; 50% protein; 30% NFE; 15% fiber and ash) (Table 9). During prelaying, however, when canvasbacks fed on tubers, the NFE component of the diet was high (68%) and the other components were low. Despite a change in the nutrient content of the diet, energy content of the diet remained remarkably constant (3.63 - 3.75 kcal/g) during all reproductive stages, including ducklings.

Contrary to the pattern observed in canvasbacks, the nutrient content of the diet of redheads fluctuated throughout the breeding season (Table 10), as did the food item composition of the diet. The diet of redheads contained more fiber and ash ($\bar{X}$=30.5%) than the diet of canvasbacks ($\bar{X}$=16.4%), a reflection of the vegetation consumed by redheads. The diet of redheads during laying was high in lipid and protein content, probably as a result of consumption of bass eggs.

The caloric content of the diet of redheads also varied (2.35 - 4.35 kcal/g) with the reproductive stage and was highest during the laying period. Despite the high lipid content and the high energy content of their diet, redheads lost about one-third (34%) of their lipid reserves during laying. Parasitic egg laying may place a

Table 9. Summary of diet and body components of female and duckling canvasbacks during the reproductive season, Ruby Lake National Wildlife Refuge, 1980-81.

	Prelaying	Laying	Incubation	Brooding	Duckling I[a]	Duckling II
DIET						
Animal (%)	7.5	77.7	77.8	88.2	85.4	89.8
Plant (%)	92.5	22.3	22.2	11.8	14.6	10.2
PREFERENCE						
Rank 1	Caddisfly	--	Caddisfly	Dragonfly	Beetles	Caddisfly
2	Dragonfly	--	Dragonfly	Caddisfly	Caddisfly	Mayfly
3	Tubers	--	Tubers	Midge	Damselfly	Midge
AGGREGATE WEIGHT						
Rank (%) 1	Tubers (84)	Caddisfly (32)	Snails (34)	Caddisfly (39)	Snails (38)	Snails (46)
2	Fungi (5)	Snails (26)	Dragunfly (22)	Dragonfly (24)	Caddisfly (21)	Dragonfly (33)
3	Dragonfly (4)	Tubers (16)	Tubers (21)	Snails (19)	Damselfly (20)	Seeds (10)
AVAILABLE FOODS						
Rank (%) 1	Seeds (52)	Veg. (52)	Seeds (46)	Snails (45)	Snails (52)	Snails (38)
2	Tubers (28)	Seeds (18)	Snails (18)	Damselfly (17)	Damselfly (13)	Damselfly (15)
3	Snails (4)	Snails (16)	Damselfly (8)	Seeds (11)	Seeds (12)	Seeds (12)
BODY COMPONENTS						
Weight (g)	1219	1255	1016	916	--	--
Lipids (g)	459	457	127	45	--	--
Protein (g)	220	226	199	178	--	--
DIET COMPONENTS						
Lipids (%)	1.5	3.5	3.3	5.0	3.8	2.9
Protein (%)	17.2	45.9	48.1	50.1	51.3	50.0
NFE (%)	67.8	34.1	32.4	27.9	26.7	30.0
Fiber & Ash (%)	13.5	16.5	16.2	17.0	18.2	17.1
Calories (KCal/g)	3.71	3.69	3.69	3.75	3.63	3.63

[a] I = Age Class I; II = Age Class II

Table 10. Summary of diet and body components of female and duckling redheads during the reproductive season, Ruby Lake National Wildlife Refuge, 1980-81.

	Prelaying	Laying	Incubation	Brooding	Duckling I[a]	Duckling II
DIET						
Animal (%)	24.6	76.8	48.6	0.6	47.2	2.1
Plant (%)	75.4	23.2	51.4	99.4	52.8	97.9
PREFERENCE						
Rank 1	Caddisfly	Bass eggs	--	--	Snails	--
2	Beetles	Caddisfly	--	--	W. Boatmen	--
3	Fungi	Dragonfly	--	--	Seeds	--
AGGREGATE WEIGHT						
Rank (%) 1	Chara (59)	Bass eggs (34)	Seeds (35)	Chara (99)	Chara (37)	Chara and
2	Seeds (8)	Dragonfly (16)	Snails (17)	--	W. Boatmen (19)	Other Veg. (92)
3	Midge (7)	Midge (12)	Chara (17)	--	Seeds (13)	Seeds (5)
AVAILABLE FOODS						
Rank (%) 1	Chara (48)	Seeds (35)	Chara (35)	Chara (90)	Chara (70)	Chara and
2	Seeds (36)	Chara (34)	Seeds (33)	W. Boatmen (3)	W. Boatmen (10)	Other Veg. (92)
3	Snails (5)	Snails (12)	Snails (17)	Tubers (2)	Snails (5)	Tubers (2)
BODY COMPONENTS						
Weight (g)	1062	1060	913	831	--	--
Lipids (g)	419	277	123	71	--	--
Protein (g)	186	201	179	156	--	--
DIET COMPONENTS						
Lipids (%)	2.9	15.1	8.1	1.0	3.8	2.4
Protein (%)	19.0	50.7	33.8	5.6	35.4	9.4
NFE (%)	43.3	19.0	39.5	48.0	31.8	48.4
Fiber & Ash (%)	34.8	15.2	18.6	45.4	29.0	39.8
Calories (KCal/g)	2.89	4.35	3.84	2.35	3.18	2.65

[a]I = Age Class I; II = Age Class II

double burden on redheads: increased egg production and increased energy expenditure of locating host nests. Additionally, redheads may be inefficient at foraging on high protein animal foods but are forced to feed on them to meet the demands of producing a large number of eggs. Thus, despite a high quality and energy rich diet during laying, redheads drew heavily upon their lipid reserves.

During incubation and brooding the diet of redheads was high in NFE, which may indicate an attempt by redheads to replenish energy reserves used during the laying period. The high NFE content of the diet during incubation and brooding may also account for the greater retention of lipid reserves during these periods relative to canvasbacks.

CONCLUSIONS

Canvasbacks pursue a relatively conservative strategy of foraging and reproduction. They consumed a mixed but consistent diet, often comprised of the most preferred foods. Canvasbacks selected a diet that provided a constant caloric intake and they retained energy reserves for expenditure during incubation and brooding.

Redheads, on the other hand, appeared to pursue an opportunistic approach to foraging and reproduction. Much of the diet of redheads was comprised of the most abundant foods. Redheads invested much energy in producing eggs and placing them in hosts' nests. Because the parasitic and semi-parasitic segments of redhead populations have adopted a strategy of utilizing much of their energy reserves during the laying period, the general contention among waterfowl biologists that redheads are "poor mothers" may be explained by the fact redheads simply do not retain enough energy reserves to allow high attentiveness to nests and broods.

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APPENDICES

Table 11. Proportion of food items in food availability samples for canvasback and redhead females and ducklings at different stages of reproduction, Ruby Lake National Wildlife Refuge, Nevada, 1980-81. Sample sizes are in parentheses.

	Dragonfly nymphs	Damselfly nymphs	Midge larvae	Snails	Caddisfly larvae	Beetles	Water Boatmen	Mayfly larvae	Pondweed tubers	Benthic vegetation*	Seeds	Phycomycete fungus	Total wt (g)
CANVASBACKS													
Prelaying (14)	0.043	0.028	0.030	0.044	0.003			0.002	0.276	0.032	0.524	0.017	10.94
Laying (6)	0.007	0.046	0.020	0.164	0.041	0.002		0.002	0.024	0.518	0.178		8.60
Incubating (12)	0.028	0.079	0.075	0.185	0.012	0.001		0.016	0.073	0.075	0.464		7.32
Brooding (7)	0.018	0.168	0.059	0.451	0.084	0.022	0.009	0.009	0.001	0.071	0.108		3.43
Age Class I (9)	0.022	0.128	0.021	0.515	0.079	0.002		0.006	0.044	0.055	0.121		4.06
Age Class II (15)	0.024	0.145	0.077	0.376	0.061	0.018	0.022	0.021	0.047	0.092	0.116		8.07
REDHEADS													
Prelaying (13)	0.002	0.018	0.024	0.048	0.002			0.002	0.020	0.482	0.359	0.042	17.80
Laying (11)	0.022	0.030	0.073	0.118	0.009	0.023		0.011	0.027	0.337	0.349		15.15
Incubating (7)	0.008	0.019	0.033	0.174	0.006	0.045		0.003	0.030	0.352	0.328		7.95
Brooding (7)	0.004	0.014				0.003	0.029	0.014	0.019	0.902	0.018		14.77
Age Class I (7)	0.030	0.011	0.038	0.054		0.006	0.104	0.043	0.003	0.702	0.009		10.19
Age Class II (8)		0.002	0.016			0.003	0.013	0.001	0.017	0.918	0.030		22.86

* Includes Chara, Zannichellia, Potamogeton

Table 12. Changes in organ weights of female canvasbacks by reproductive stage, Ruby Lake National Wildlife Refuge, Nevada, 1980-81. Sample sizes are in parentheses.

	Prelaying		Laying		Incubating		Brooding
Weight (g)	(mean ± SE)	P[a]	(mean ± SE)	P	(mean ± SE)	P	(mean ± SE)
Gizzard	33.0 ± 2.0 (18)	*	26.5 ± 0.9 (6)	NS	26.0 ± 1.9 (12)	NS	24.4 ± 3.1 (8)
Heart	13.5 0.4 (18)	*	11.4 0.6 (6)	NS	11.1 0.5 (12)	*	9.2 0.8 (8)
Liver	34.6 1.8 (18)	NS	37.3 1.8 (6)	NS	33.6 1.9 (12)	*	27.0 1.6 (8)
Ovary	4.1 1.8 (18)	***	40.3 4.8 (6)	***	1.5 0.3 (12)	**	0.4 0.1 (6)
Oviduct	6.6 2.1 (18)	***	35.8 2.3 (6)	***	4.0 0.7 (12)	*	1.1 0.1 (6)

[a] Significance level of t-test between means in adjacent columns. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS represents $P > 0.05$.

Table 13. Changes in organ weights of female redheads by reproductive stage, Ruby Lake National Wildlife Refuge, Nevada, 1980-81. Sample sizes are in parentheses.

	Prelaying		Laying		Incubating		Brooding
Weight (g)	(mean ± SE)	P[a]	(mean ± SE)	P	(mean ± SE)	P	(mean ± SE)
Gizzard	72.9 ± 3.3 (15)	NS	68.8 ± 5.4 (14)	NS	74.0 ± 7.8 (8)	*	54.4 ± 3.9 (8)
Heart	10.3 0.2 (15)	***	9.1 0.2 (14)	NS	8.5 0.4 (8)	NS	7.6 0.3 (8)
Liver	25.8 1.5 (15)	*	31.1 1.4 (14)	*	25.0 1.5 (8)	**	19.1 1.1 (8)
Ovary	5.1 2.1 (15)	***	32.7 4.5 (14)	***	2.6 0.6 (8)	**	0.4 0.1 (7)
Oviduct	6.5 1.7 (14)	***	35.4 1.6 (13)	***	8.6 2.4 (8)	*	0.8 0.1 (5)

[a] Significance level of t-test between means in adjacent columns. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS represents $P > 0.05$.

Table 14. Changes in organ weights of male canvasbacks and redheads by reproductive stage, Ruby Lake National Wildlife Refuge, 1980-81. Sample sizes are in parentheses.

	CANVASBACKS			REDHEADS		
	Prelaying		Laying	Prelaying		Laying
Weight (g)	(mean ± SE)	P[a]	(mean ± SE)	(mean ± SE)	P	(mean ± SE)
Gizzard	37.2 ± 1.6 (8)	NS	33.1 ± 4.6 (4)	81.6 ± 6.1 (8)	NS	73.0 ± 8.3 (5)
Heart	14.0 ± 0.3 (8)	NS	13.8 ± 0.9 (4)	10.4 ± 0.3 (8)	NS	9.4 ± 0.5 (5)
Liver	32.3 ± 2.9 (8)	NS	28.4 ± 2.6 (4)	22.5 ± 0.8 (8)	**	18.2 ± 1.3 (5)
Testes	4.9 ± 1.1 (6)	*	8.5 ± 0.7 (4)	3.3 ± 0.7 (8)	**	6.6 ± 0.4 (5)

[a] Significance level of t-test between means in adjacent columns. * = $P < 0.05$; ** = $P < 0.01$; NS represents $P > 0.05$.