

# NUTRIENT RESERVE DYNAMICS OF BREEDING CANVASBACKS

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**ABSTRACT.**—We compared nutrients in reproductive and nonreproductive tissues of breeding Canvasbacks (*Aythya valisineria*) to assess the relative importance of endogenous reserves and exogenous foods. Fat reserves of females increased during rapid follicle growth and varied more widely in size during the early phase of this period. Females began laying with ca. 205 g of fat in reserve and lost 1.8 g of carcass fat for every 1 g of fat contained in their ovary and eggs. Females lost body mass (primarily fat) at a declining rate as incubation advanced. Protein reserves increased directly with dry oviduct mass during rapid follicle growth. This direct relationship was highly dependent upon data from 2 birds and likely biased by structural size. During laying, protein reserves did not vary with the combined mass of dry oviduct and dry egg protein. Between laying and incubation, mean protein reserves decreased by an amount equal to the protein found in 2.1 Canvasback eggs. Calcium reserves did not vary with the cumulative total of calcium deposited in eggs. Mean calcium reserve declined by the equivalent content of 1.2 eggs between laying and incubation. We believe that protein and calcium were stored in small amounts during laying, and that they were supplemented continually by exogenous sources. In contrast, fat was stored in large amounts and contributed significantly to egg production and body maintenance. Male Canvasbacks lost fat steadily—but not protein or calcium—as the breeding season progressed. Received 12 April 1988, accepted 22 July 1989.

MOST arctic-nesting geese acquire nutrients and energy (included here as a nutrient) for reproduction before they arrive on breeding grounds where food is not available early in the breeding season (e.g. Ankney and MacInnes 1978, Raveling 1979, Wypkema and Ankney 1979). Conversely, temperate species of waterfowl nest where food is available throughout the reproductive period, and nutrients used for egg production or incubation presumably come from both endogenous and exogenous sources (e.g. Drobney 1980, Krapu 1981, Ankney and Afton 1988).

Rohwer (1986) observed declines in nutrient reserves as female Blue-winged Teal (*Anas discors*) laid eggs, but he did not conclude that nutrient reserves influenced reproductive success. Instead, Rohwer (1986: 37) suggested that "Migrating waterfowl may simply store fat to assure that they have the energy for migration

and as a hedge against unfavorable weather upon arrival at the breeding grounds." If true, the use of nutrient reserves for reproduction would be of secondary importance and not a large factor influencing reproductive success.

Variation in body size among anatids partially explains the extent to which endogenous reserves are used for reproduction (Afton 1979, 1980; Ankney 1984; but see Dobush 1986). We believe that, until the use of reserves can be studied in larger species, extending Rohwer's conclusions to other waterfowl would be premature. Krapu (1974, 1981) argued that large-bodied, early-nesting Northern Pintails (*A. acuta*) and Mallards (*A. platyrhynchos*) must forage on scarce invertebrates to meet protein requirements of egg production. He suggested that fat reserves were mobilized for body metabolism and for deposition in follicles. We feel Krapu's results only weakly support his hypothesis. If fat reserves are used for both body maintenance and egg production, fat reserves should decline faster than they appear in reproductive tissue. For Mallards, loss of body fat during laying could account for fat found in a clutch, but it could not account for additional fat metabolized for body maintenance (Krapu 1981).

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Canvasbacks (*Aythya valisineria*) are large ducks that initiate nests early in spring soon after arrival (Anderson 1985b) and have a short breeding period (Doty et al. 1984). Nutrient reserves might therefore influence annual productivity. We described the dynamics of fat, protein, and calcium reserves in breeding Canvasbacks. For those reserves that appear to vary with reproduction, we examined three predictions developed from Rohwer's (1986) explanation of why reserves decline in breeding ducks. First, if reserves are required during spring migration, then the decline of those reserves in breeding birds should be related to date rather than stage of reproduction. Second, once migration is complete, reserves should decline rather than be maintained for later reproductive needs. Third, reserves should not be reacquired before renesting.

#### METHODS

Breeding Canvasbacks were collected, or captured on nests (Weller 1957), randomly near Minnedosa, Manitoba, from 1977 to 1981. An additional female was collected in 1984. For descriptions of the study area, see Stoult (1982). After collection, all birds were weighed to 1.0 g, aged by plumage characteristics as second year (SY) or after second year (ASY) (Serie et al. 1982), and dissected for food analysis (J. E. Austin et al. MS). Reproductive tissue was removed and weighed to 0.1 g. Ovaries were placed in alcohol, but oviducts and testes were frozen with the carcass.

To determine reproductive status of females, ovaries were examined with a 10× dissecting microscope, and the three largest follicle diameters were measured to 0.1 mm. Males were assigned the same status as their mate (2 males shot accidentally were of unknown status). Females were assigned to reproductive categories using the following criteria:

*Pre-rapid follicle growth.* Largest follicle diameter is less than 7.5 mm.

*Rapid follicle growth.* Largest follicle diameter is greater than or equal to 7.5 mm, and no post-ovulatory follicles are present.

*Laying.* Postovulatory follicles are present, and there is at least one developing follicle in the ovary or an egg in the oviduct.

*Incubation.* Brood patch is evident on the female, postovulatory follicles are present, and largest follicle diameter is less than 12.0 mm.

*Renesting, rapid follicle growth.* Brood patch or post-ovulatory follicles are still evident, and follicles are developing (largest follicle diameters are greater than or equal to 12.0 mm).

Yolk deposition begins the rapid growth phase of

follicles (Gilbert 1971), when follicle color changes from gray to yellow (Romanoff and Romanoff 1949). We could not use color to determine when rapid follicle growth began because ovaries were stored in alcohol. No female among 12 early-breeding Canvasbacks in another study had a yellow follicle <7.5 mm in diameter (Barzen 1989). In our sample, no female that laid her last egg had a follicle >12 mm in diameter ( $\bar{x} = 8.5 \pm 3.3$  mm [95% CL],  $n = 4$ ). This parallels patterns reported in renesting captive Mallards (Donham et al. 1976).

We could not determine the incubation stage for collected birds. But body mass of 8 after-second-year females and 2 second-year females predicted fat mass well (fat mass =  $-102.4 + 0.12$  [body mass];  $S_b = 0.02$ ,  $r^2 = 0.80$ ,  $P = 0.0004$ ). Therefore we used the body mass of females captured on nests to estimate changes in fat reserves during incubation. We used 90 females from this study and 117 females captured later on the same area (M. G. Anderson and M. D. Sorenson pers. comm.). We estimated incubation stage for captured females from 2–3 candled eggs from each nest (Weller 1956) or by back-dating from known hatching dates.

*Body composition.*—We removed the bill, tongue, scaled portion of the feet, feathers, intestinal contents, and reproductive tissue from the thawed carcass. Carcasses were refrozen and ground 3 times, then homogenized in a blender. A 30–50 g random sample was withdrawn from the wet homogenate, dried to constant mass at 75°C, and then ground to a powder. Fat was extracted in petroleum ether (Dobush et al. 1985) from two 3-g subsamples per bird in a Randall extraction apparatus (Randall 1974) after the homogenate powder was dried to constant mass at 90°C (Kerr et al. 1982).

We estimated protein reserves by ashing the two extracted subsamples to constant mass at 600°C. Carbohydrates and lipids not extracted by ether (e.g. phospholipids) were included in this estimate, but they composed a relatively small proportion of the tissue (Drobney 1982, Robbins 1983). Remaining ash was dissolved in concentrated nitric acid, diluted with deionized water and lithium chloride, and analyzed for calcium in a plasma emission spectrometer (Reednick 1979). Mineral mass was calculated as ash mass minus calcium mass. Medullary tissue was estimated during dissection by scoring the extent of medullary tissue in a cross section of the mid-left femur. We followed categories of Campbell and Leatherland (1983) except that we reversed their order of scoring: thus 1 = least medullary tissue; 3 = most.

Internal organs of 8 after-second-year females and 1 male were not returned to the carcass after field dissection. Omission of these organs biased protein reserve estimates so these birds were excluded from protein analysis. Fat that adhered to these organs was removed, and no organs contained bone fragments. Estimates of fat and calcium reserves should not be biased.

TABLE 1. Body composition and reproductive tissue ( $\bar{x} \pm SD$ ) of after-second-year female Canvasbacks during first and subsequent nesting attempts. Sample sizes are in parentheses, RFG = rapid follicle growth.

Variable <sup>a</sup>	Pre-RFG (2) <sup>b</sup>	P <sup>c</sup>	RFG (15) <sup>d</sup>	P <sup>c</sup>	Laying (14) <sup>e</sup>	P <sup>c</sup>	Incubation (8) <sup>f</sup>	Restesting, RFG (8) <sup>g</sup>	P <sup>h</sup>
Fresh body mass	1,250 ± 71	NS	1,387 ± 111	NS	1,452 ± 85	***	1,117 ± 147	1,381 ± 135	NS
Dry body mass	283.2 ± 1.6	***	398.7 ± 51.9	NS	378.5 ± 27.5	***	273.4 ± 32.9	366.4 ± 50.0	NS
Fat mass	56.3 ± 14.2	***	149.1 ± 36.2	*	122.3 ± 29.9	***	39.1 ± 19.6	113.2 ± 40.7	*
Protein mass	—		213.0 ± 17.0	NS	213.1 ± 5.6	***	193.7 ± 18.2	210.3 ± 10.9	NS
Calcium mass	10.1 ± 0.3	NS	11.8 ± 1.9	NS	13.2 ± 2.3	NS	11.8 ± 1.2	13.2 ± 2.4	NS
Mineral mass	25.2 ± 1.3	NS	28.9 ± 4.2	NS	31.8 ± 4.6	NS	28.8 ± 2.6	31.5 ± 4.5	NS
Medullary tissue	0.0 ± 0.0	*	1.0 ± 0.8	**	2.2 ± 0.6	***	0.4 ± 0.7	1.7 ± 1.1	NS
Ovary mass <sup>i</sup>	1.3 ± 0.3	NS	17.5 ± 17.3	NS	34.4 ± 20.4	***	1.6 ± 1.2	22.2 ± 15.4	NS
Oviduct mass <sup>j</sup>	3.4 ± 1.7	***	18.7 ± 9.6	***	38.2 ± 5.4	***	5.9 ± 4.7	25.5 ± 10.9	NS
Largest follicle	6.0 ± 0.6	**	19.5 ± 11.6	*	33.3 ± 11.8	***	4.9 ± 2.7	27.5 ± 9.5	NS

<sup>a</sup> Measurements of mass are in g, medullary tissue is an index, and largest follicle is a measure of diameter in mm.

<sup>b</sup>  $n = 0$  for protein mass.

<sup>c</sup>  $P =$  probability (from one-way ANOVA) that means of adjacent columns are different by chance. NS =  $P > 0.10$ ; \* =  $0.05 < P \leq 0.10$ , \*\* =  $0.01 < P \leq 0.05$ , and \*\*\* =  $P \leq 0.01$ .

<sup>d</sup>  $n = 12$  for fresh body mass,  $n = 11$  for protein mass, and  $n = 14$  for ovary mass.

<sup>e</sup>  $n = 13$  for protein mass and largest follicle.

<sup>f</sup>  $n = 7$  for ovary mass.

<sup>g</sup>  $n = 7$  for protein mass and medullary tissue.

<sup>h</sup>  $P =$  probability that means of "rapid follicle growth" and "retesting, rapid follicle growth" are different by chance.

<sup>i</sup> Wet mass.

**Reproductive tissue.**—We analyzed each ovary for fat by drying it to constant mass, grinding it with a pestle, and extracting as above. We recovered fat dissolved by the alcohol in storage jars. We did not measure ovary protein and calcium.

Oviducts were assumed to consist primarily of protein and water (Romanoff and Romanoff 1949). Measurements of fresh oviduct mass were missing for 27 of 59 females, and desiccation of frozen oviducts was evident. For these 27 birds, fresh oviduct mass was estimated by regression (fresh mass =  $0 + 1.32$  [lab mass];  $n = 32$ ,  $S_b = 0.03$ ,  $r^2 = 0.93$ ,  $P = 0.0001$ ). Masses of dry oviducts were calculated as fresh mass multiplied by 0.2 (C. D. Ankney pers. comm.).

Twelve unincubated eggs were collected from 2 nests in 1985, weighed to the nearest 0.1 g, boiled, frozen, and later thawed for analysis. These eggs averaged ( $\bar{x} \pm SD$ ) 68.0 ± 3.1 g fresh mass, 8.5 ± 0.6 g fat mass, 9.1 ± 0.4 g protein mass, and 2.5 ± 0.2 g calcium mass. The values were incorporated into estimates of total nutrients committed to reproductive tissue following Alisauskas and Ankney (1985): reproductive fat = fat in ovary + (number of postovulatory follicles × mean fat per egg); protein = dry mass of oviduct + (number of postovulatory follicles × mean protein per egg); calcium = number of postovulatory follicles × mean calcium per egg.

**Statistical analysis.**—Least-squares regression was used in all regression analyses (SAS 1985). For incubating females, heterogeneity of slopes among age and nesting status (initial vs. retesting birds) combinations were tested using dummy variable and regression techniques. When slopes were similar, ANCOVA was used to test for equality of intercepts (Sokal and Rohlf 1981). One-way ANOVA and Dun-

can's new multiple range test were used to compare means from adjacent stages of reproduction (SAS 1985). Unplanned comparisons of nonadjacent means were tested with the Tukey-Kramer procedure (Sokal and Rohlf 1981).

## RESULTS

### FEMALES

Although mean body mass of 49 females appeared to change through the reproductive period, few interval differences were significant (Table 1). Body mass tended to increase from pre-rapid follicle growth through laying, and it decreased significantly between laying and incubation (Table 1). Mean dry body mass and fat reserves peaked during rapid follicle growth rather than laying. Protein reserves and medullary tissue declined significantly between laying and incubation. Overall changes imply a general peak in nutrient reserves in late rapid follicle growth or early laying followed by a general decline through incubation.

Comparisons of mean nutrient reserves are difficult to interpret because females were collected at different times within each stage of reproduction. Accordingly, like Alisauskas and Ankney (1985), we compared the amount of a specific nutrient found in somatic tissue (nutrient reserve) with the amount of that nutrient found in reproductive tissue (reproductive nutrient). Their model predicts a negative rela-

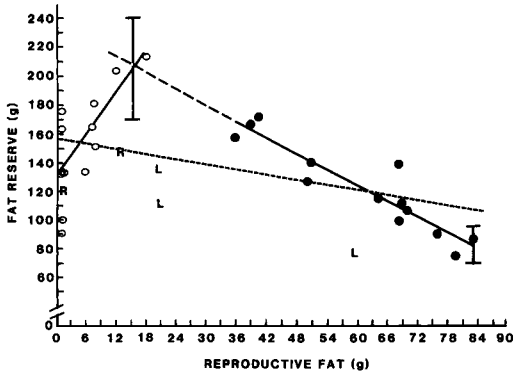


Fig. 1. Fat reserve mass and reproductive fat for after-second-year (ASY) female Canvasbacks on their initial nesting attempt. Solid lines denote regressions within each stage of reproduction. The dotted line incorporates both stages of reproduction; the dashed line extrapolates between the laying and rapid follicle growth (RFG) model to estimate the point of inflection. Vertical bars are 95% confidence limits. Values from second-year (SY) females are plotted for comparison.  $\circ$  = RFG, ASY ( $y = 130.4 + 5.01x$ ;  $r^2 = 0.56$ ,  $S_b = 1.34$ ,  $P = 0.003$ );  $\bullet$  = laying, ASY ( $y = 231.6 - 1.80x$ ,  $r^2 = 0.86$ ,  $S_b = 0.22$ ,  $P = 0.0001$ );  $\circ$  = RFG, SY;  $\circ$  = laying, SY.

relationship between nutrient reserves ( $y$ ) and nutrients committed to reproduction ( $x$ ), if reserves are used for reproduction.

*Fat reserves and body mass.*—Canvasbacks lost fat from reserves as reproductive fat was acquired when rapid follicle growth and laying periods were combined ( $y = 157.1 - 0.61x$ ;  $n = 26$ ,  $S_b = 0.20$ ,  $r^2 = 0.27$ ,  $P = 0.006$ ). This relationship clearly differed between the 2 stages of reproduction (Fig. 1). A polynomial model ( $y = 132.8 + 5.5x - 0.15x^2 + 0.001x^3$ ) explained a greater variance ( $n = 26$ ,  $r^2 = 0.68$ ,  $P = 0.0001$ ), but it was difficult to interpret. We used separate regressions for each stage of reproduction (Fig. 1).

We estimated that, during rapid follicle growth, most (99%) follicle growth occurred over 7 days. Through rapid follicle growth, an average female Canvasback increased fat reserves by 70 g and simultaneously added 20 g of reproductive fat (Fig. 1). An increase of 12.8 g/day of fat parallels an increase in body mass of 51.2 g/day. Variances in fat reserves were large early in rapid follicle growth and small later in the period. Thus, confidence limits underestimate fat reserve values early and overestimates them later. The slope of this regression appears high-

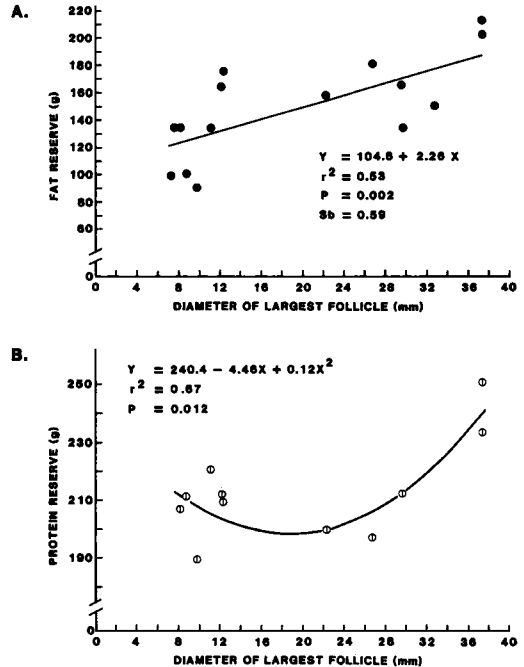


Fig. 2. Regression of fat reserve (A) and protein reserve (B) on largest follicle diameter during rapid follicle growth for after-second-year female Canvasbacks, initial nesting attempt.

ly dependent upon values for 2 birds collected late in rapid follicle growth (Fig. 1). Fat reserves also varied with the largest follicle diameter (Fig. 2A). However, values along the abscissa were not aggregated near zero, and variances were similar throughout rapid follicle growth. Follicle diameter is a more sensitive indicator of early reproductive development than is fat content of the ovary (Fig. 2A).

Laying after-second-year birds lost 1.8 g fat from their reserve for every gram committed to reproduction (Fig. 1). If fat reserves were mobilized only to be deposited in follicles, and if efficiency of converting fat from reserves to reproductive fat was near 100%, the slope would approximate  $-1.0$  (Rohwer 1986). Our slope (Fig. 1) differed from this predicted value (one-tailed test,  $F = 13.12$ ,  $P = 0.002$ ,  $n = 13$ ), which suggests that fat reserves were used for both egg production and other metabolic functions.

We estimated that females ended rapid follicle growth with a fat reserve of ca. 205 g by extrapolating between the models for females during laying and rapid follicle growth (Fig. 1). The 95% confidence interval for this point

(170–240 g) is biased because variances in the rapid follicle growth model were large early, and small late, in the period. In late rapid follicle growth, this bias would inflate the confidence interval and therefore would be conservative. By the end of laying, females had 83 g of fat in reserve (95% CL = 70–96 g) and had lost about 122 g of fat through laying. Of this loss, 69.7 g could have been mobilized for deposition in 8.2 eggs (mean clutch size for early nests; Stoult 1982), and 52.3 g could have been used for other metabolic functions. Fifty-two grams of fat could fuel a fasting female at rest no more than 4.4 days (using mean fresh body mass of laying females = 1,452 g [Table 1]; 39.54 kJ/g of fat [Ricklefs 1974]; Aschoff and Pohl's [1970] estimate of standard metabolic rate for nonpasserines; and assuming an 8:16 h ratio of rest to active periods). Laying females are highly active (Anderson 1985b), so reserves would last for a shorter period.

If fat reserves are necessary for reproduction, reneesting females should reacquire fat deposits before initiating new nests (assuming the availability of food remains constant throughout the breeding season). Fat reserves of reneesting after-second-year females with developing follicles were unrelated to ovary fat ( $n = 8$ ,  $r^2 = 0.20$ ,  $P = 0.27$ ). All but one bird had fat reserves lower than the range of females initiating their first clutch.

If fat reserves were lost during reneesting in a way similar to birds laying their initial clutch (Fig. 1), a difference in fat reserves of 35.9 g between rapid follicle growth and reneesting, rapid follicle growth birds (Table 1) would decrease reproductive fat by 20.0 g. This could reduce the clutch size of reneesting birds by 2.4 eggs. Three reneesting females, collected 1–2 days from ovulation (largest follicle diameter  $\geq 31$  mm), had fat reserves of 175.0 g, 134.4 g, and 66.6 g. If mobilized solely for egg production, 67 g of fat could produce the 7–8 eggs expected in a reneesting attempt but would leave no fat in reserve, an unlikely event. One radio-marked female, who had just abandoned her third nesting attempt in a minimum of 33 days, had 30 g of body fat. She had committed 110.5 g of fat to reproduction (13 ruptured follicles). When incorporated into the model for females laying their first clutch (which did not include this bird), her predicted fat reserve was 33.0 g.

Too few second-year females were collected to analyze quantitatively. Laying SY females may

have used fat as did ASY females, but SY females tended to begin laying with smaller fat reserves (Fig. 1).

In their initial nesting attempt, ASY females began incubation at an average body mass of 1,157 g (95% CL = 1,119–1,195 g). They lost mass at a declining rate as incubation progressed (Fig. 3). A body mass of 1,157 g correlates with 42 g of fat (95% CL = 37–47 g). The predicted 95% confidence interval for fat reserves in late laying (53–112 g; Fig. 1) did not overlap this interval. Underestimation of fat mass might have been due to reproductive tissue regressing independently of fat reserves early in incubation. Consequently, we used 83 g of fat to estimate fat reserves at the beginning of incubation (Fig. 1), and we used regression to estimate fat reserves from body mass late in incubation.

A 1,157-g Canvasback starting incubation would lose 10.0 g/day of fat to meet standard metabolic demands (using the same assumptions as above) and 3.16 g/day of fat to incubate (using Kendeigh's [1963] equation for cost of incubation, and Caldwell and Cornwell's [1975] estimates of incubation parameters except clutch size = 8.2, egg mass = 70.4 g, and incubation constancy = 92%). We have no estimates for energy expended by females during recesses. A loss of 13.2 g/day of fat would allow an incubating female to fast a maximum of 6.3 days (26% of incubation period). At hatch, ASY females in their initial nesting attempt had an average mass of 1,001 g (95% CL = 981.7–1,020.9 g). This corresponds to 23 g of fat (95% CL = 20–25 g), a decrease of 72% from their estimated reserves available at the start of incubation. Mean body fat of 8 incubating females was 39.1 g (Table 1).

To compare changes in female body mass among combinations of age and nesting status, natural log transformations of body mass ( $y$ ) and stage of incubation ( $x$ ) were made to allow straight-line comparisons. Values for each model were (1) ASY, initial nest attempt,  $\ln(y) = 7.08 - 0.052 \ln(x)$ ,  $r^2 = 0.32$ ,  $P = 0.0001$ ,  $n = 148$ ; (2) ASY, reneesting,  $\ln(y) = 7.00 - 0.023 \ln(x)$ ,  $r^2 = 0.16$ ,  $P = 0.04$ ,  $n = 27$ ; (3) SY, initial nest attempt,  $\ln(y) = 7.13 - 0.087 \ln(x)$ ,  $r^2 = 0.38$ ,  $P = 0.0009$ ,  $n = 26$ ; and (4) SY, reneesters,  $r^2 = 0.09$ ,  $P = 0.56$ ,  $n = 6$ . Age had no effect on rate of mass loss when first and subsequent nests were combined ( $P = 0.56$ ). After-second-year and second-year females also did not differ in body mass at the start of incubation ( $P = 0.74$ ).

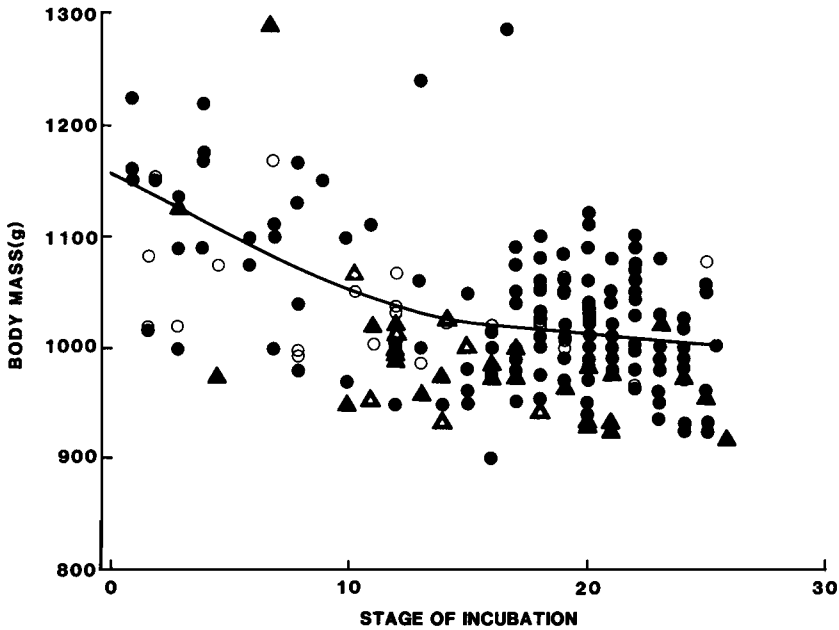


Fig. 3. Body mass ( $y$ ) plotted against stage of incubation ( $x$ ) for female Canvasbacks. ● = after-second-year (ASY) females, initial nesting attempt; ○ = ASY females, renesting; ▲ = second-year (SY) females, initial nesting attempt; and △ = SY females, renesting. The regression for ASY females, initial nesting attempt ( $y = 1157 - 11.8x + 0.2x^2$ ), has been graphed.

Birds incubating first and subsequent nests lost body mass at the same rate ( $P = 0.71$ ), but re-nesting females initiated incubation at a lower body mass ( $P = 0.0001$ ). Some interaction between age and nesting status is likely because few (6 of 32) SY females that lost their first nest attempted to renest.

*Protein reserves.*—Protein reserves were not related to reproductive protein when laying and rapid follicle growth periods were combined ( $n = 22$ ,  $r^2 = 0.003$ ,  $P = 0.82$ ). Protein reserves changed directly with reproductive protein during rapid follicle growth but not during laying (Fig. 4A). As with fat, the significance of the rapid follicle growth model was highly dependent upon two values. We plotted protein reserve mass on largest follicle diameter (Fig. 2B) and found that the model explained a significant amount of variation. Unlike the model in Fig. 2A, this relationship was still strongly dependent upon the values for two birds. Thus, structural size or some other factor independent of reproduction may have biased our results. Incubating females had 19.4 g less protein than did laying females (Table 1). This difference equals 2.1 times the amount of protein found in a Canvasback egg (9.1 g).

Mean protein reserves of rapid follicle growth females and renesting rapid follicle growth birds did not differ (Table 1). Protein reserves and dry oviduct mass of renesting females were not related ( $n = 8$ ,  $r^2 = 0.28$ ,  $P = 0.18$ ). The 192-g protein reserve mass of the radio-marked female was similar to incubating females (Table 1). Second-year females tended to have lower protein reserves than ASY females, but their pattern of reserve use was similar (Fig. 4A).

Protein reserve mass of incubating females was unrelated to body mass ( $n = 10$ ,  $r^2 = 0.06$ ,  $P = 0.50$ ). Comparisons between incubation stage and protein reserve were not possible. The only renesting female collected during incubation had a protein mass of 208 g, which was close to that of females incubating their first clutch (Table 1).

*Calcium reserve mass vs. reproductive calcium.*—No relationship between calcium reserves and reproductive calcium was found (Fig. 4B). Medullary tissue changed significantly through most of the reproductive period (Table 1). This paralleled nonsignificant trends in calcium and mineral reserves. The difference in calcium reserve between pre-rapid follicle growth and laying females was 3.1 g (unplanned compari-

son,  $P = 0.1$ ). This value approximates the calcium found in one Canvasback egg (2.5 g). Calcium reserves of SY and ASY females were similar (Fig. 4B).

## MALES

Throughout reproduction, measures of body composition in 19 males changed little (Table 2). Males had no medullary tissue and lost fat from their reserves as the season progressed, independent of their reproductive status (Fig. 5A). Neither protein nor calcium reserves were related to Julian date (Fig. 5: B, C).

## DISCUSSION

*Nutrient reserve use.*—Increases in fat reserves after arrival, but before laying, have been shown previously in Wood Ducks (*Aix sponsa*; Drobney 1982, Drobney and Fredrickson 1985) and Ruddy Ducks (*Oxyura jamaicensis*; Tome 1984). During rapid follicle growth, female Canvasbacks increased their mass at ca. 51 g/day, of which 12.8 g was fat. In comparison, fresh body mass of migrant Lesser Scaup (*Aythya affinis*) in autumn increased at a maximum of 32–44 g/day (A. Afton in prep.). Takekawa (1987) estimated that captive Canvasbacks could gain 32.4 g/day of fat during autumn migration.

Our measurement of rapid follicle growth was indirect. Errors in this estimate would bias the rates for mass gain. In another sample, 10 of 11 Canvasbacks collected soon after arrival had initiated rapid follicle growth (Barzen 1989). If rapid follicle growth began upon arrival, the first egg could be laid 8 days later (7 days for rapid follicle growth + 1 day for shell calcification). Excluding a drought year, Anderson (1985b, pers. comm.) reported an average interval of 13.1 days between the first day a marked after-second-year Canvasback was seen on the breeding grounds and the day that bird's first egg was laid. Yet our estimate of 7 days is similar in pattern and length to follicle growth of "ducks" (Romanoff and Romanoff 1949). Length of this period also agrees with minimum renest intervals calculated for Canvasbacks (Doty et al. 1984 following Donham et al. 1976). The use of a change in follicle color to define rapid follicle growth initiation may include a period of time when follicle growth is slow or suspended. It

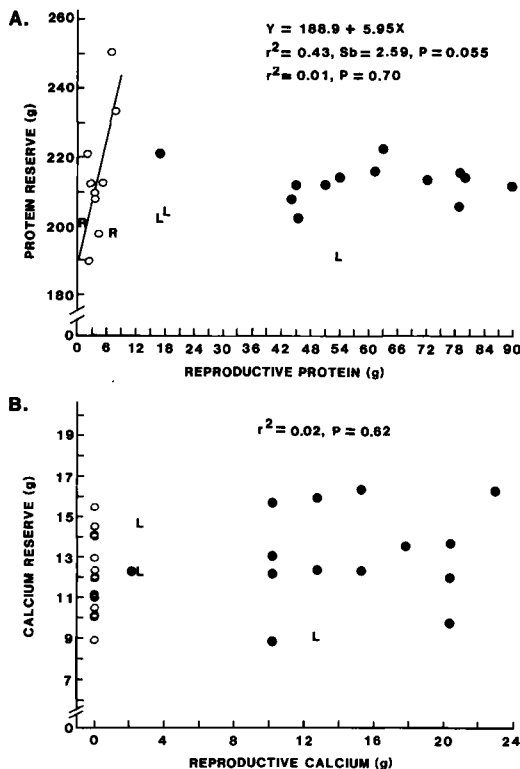


Fig. 4. Regression of protein (A) and calcium (B) reserves on the level of that nutrient committed to reproductive tissue for after-second-year (ASY) female Canvasbacks, initial nesting attempt. Values from second year (SY) females are plotted for comparison. O = rapid follicle growth (RFG), ASY; ● = laying, ASY; R = RFG, SY; L = laying, SY.

still takes 7 days for *most* follicle growth to occur, but follicles may yellow before this rapid growth period. With a 13-day interval between arrival and laying to estimate the length of rapid follicle growth, we calculated that the rate of fat and body-mass gain would decrease to 6.9 and 27.6 g/day, respectively.

Not all females may acquire fat reserves during rapid follicle growth before they ovulate. Some Canvasbacks began rapid follicle growth with large reserves, close to or above the level at which other birds began laying (Fig. 1). Other females began rapid follicle growth relatively lean. In 1984, 11 after-second-year females collected soon after arrival ranged from 125 to 230 g of fat mass (Barzen 1989). Among-year variation cannot be the only explanation for variations in body mass. After-second-year females may enter early stages of rapid follicle growth

TABLE 2. Body composition ( $\bar{x} \pm SD$ ) of after-second-year male Canvasbacks accompanying mates making their first and subsequent nesting attempts. Sample sizes are in parentheses.

Tissue mass (g)	Pre-rapid follicle growth (1)	$P^a$	Rapid follicle growth (8) <sup>b</sup>	$P^a$	Laying (4)	$P^a$	Incubation (1)	Renesting, rapid follicle growth (3)	$P^c$
Fresh body mass	1,520	***	1,280 $\pm$ 48	NS	1,280 $\pm$ 72	NS	1,200	1,237 $\pm$ 23	NS
Dry body mass	515.0	***	371.4 $\pm$ 54.7	NS	345.4 $\pm$ 21.0	NS	344.6	354.9 $\pm$ 26.5	NS
Fat mass	256.8	***	116.7 $\pm$ 45.6	NS	98.9 $\pm$ 26.6	NS	82.7	110.1 $\pm$ 24.7	NS
Protein mass	213.4	NS	211.0 $\pm$ 8.0	NS	203.0 $\pm$ 7.2	*	217.8	202.8 $\pm$ 4.3	NS
Calcium mass	13.3	NS	12.8 $\pm$ 2.5	NS	12.9 $\pm$ 1.2	NS	13.4	12.4 $\pm$ 0.3	NS
Mineral mass	31.4	NS	31.4 $\pm$ 5.1	NS	30.6 $\pm$ 3.0	NS	30.8	29.6 $\pm$ 1.0	NS

<sup>a</sup> Probability that means in adjacent columns are different by chance (see Table 1).

<sup>b</sup>  $n = 7$  for fresh body and protein reserve.

<sup>c</sup> Probability that means "rapid follicle growth" and "renesting, rapid follicle growth" are different by chance (see Table 1).

shortly after arriving on the breeding area. If fat enough to begin laying, they could continue rapid follicle growth and ovulate in 7 days. Two of 23 ASY female Canvasbacks began laying 7 and 8 days after being first seen on their breeding area (Anderson 1985b). If females arrive lean, we speculate that the early stages of rapid follicle growth may occur slowly or be suspended. The more rapid stages of follicular growth would not begin until fat reserves were greater or until food availability increased enough to reduce dependence on stored reserves.

Loss of fat during laying could account for all of the fat required to lay a clutch of eggs plus additional energy for body maintenance. These results are consistent with, but cannot distinguish between, two hypotheses. First, laying females making their initial nesting attempt must use stored energy to produce eggs and to compensate for feeding intensively on invertebrates as a source of protein (Krapu 1974, 1981; Drobney 1980, 1982). Alternatively, energy content—not the protein content—of the diet, is limiting to laying females and requires use of fat reserves (Ankney and Afton 1988). In Nevada, laying female Canvasbacks fed primarily on invertebrates (Noyes and Jarvis 1985), even though their mates consumed tubers (Jarvis and Noyes 1986). Females from this study ate both tubers and invertebrates (J. E. Austin et al. MS). Other factors besides availability of protein or energy sources may constrain a female's time to feed and thus require use of reserves. For example, Canvasbacks nest over the water and spend from 6 h/day at the nest in early laying to 14 h/day in late laying (Anderson 1985b). This might limit their time available for foraging.

We found a strong relationship between fat reserves and reproductive fat during laying. In contrast, Noyes and Jarvis (1985) reported fat reserves of Canvasbacks were used primarily during incubation. Of 17 pre-laying females, only one had a fresh ovary mass  $>9.2$  g. In addition, in four ASY laying females, two had laid 4 eggs, one had laid 5, and one had laid an unknown number of eggs (J. H. Noyes and R. L. Jarvis pers. comm.). If a period from early rapid follicle growth to mid-laying was eliminated from our data, we could not have demonstrated fat loss during laying (Fig. 1).

Canvasbacks lost an average of 13.5% of their body mass during incubation (Fig. 3). Following Ankney and Afton (1988), we calculated that the net gain of energy from lost body mass accounted for 24% (2,869 kJ) of the energy needed during this period. Renesting Canvasbacks began incubation at lower body mass than initial nesters, but they lost mass at a similar rate. Reduced availability of reserves therefore could be compensated for by feeding. Because our data were obtained over many years and over a wide range of environmental conditions, our results may underestimate dependence on reserves for some individuals, as Gatti (1983) found with Mallards. Alternatively, a reduction of fat reserves during incubation could reflect opportunistic use of available fat (see Rohwer 1986) or be adaptive for reasons other than maintaining incubation constancy (Freed 1981, King and Murphy 1985).

Neither calcium nor protein reserves were related to changes of these nutrients in reproductive tissue (Fig. 4). Protein reserves, however, differed by stage of reproduction, with a loss from laying to incubation equaling twice



the protein found in one egg. Protein reserves of chickens are of similar size (Scott 1973) and, in several bird species, such reserves can be mobilized for egg production (e.g. Fisher 1967, Jones and Ward 1976).

Calcium reserves appeared to peak during laying (Table 1) and declined by incubation to levels found in females during spring migration (Barzen 1989). Changes in our index of medullary tissue paralleled calcium (Table 1), which suggests that exogenous calcium was incorporated into medullary tissue and used to calcify shells (Simkiss 1967, Gilbert 1983). The size of this reserve approximates the calcium content of 1 egg or 15.1% of the calcium needed for an 8.2-egg clutch.

Compared with initial nesters, renesting female Canvasbacks had less fat but similar protein and calcium reserves during rapid follicle growth (Table 1). As with Mallards and Blue-winged Teals (Krapu 1981, Rohwer 1986), we found no evidence that Canvasbacks reacquire fat before renesting. Renesting females, however, still had large fat reserves relative to potential future clutches whereas Mallards and Blue-winged Teals did not. Other factors, such as the timing of initial nest loss or seasonal availability of food, may strongly influence patterns of reserve use by renesting birds.

Males lost fat during the reproductive period as calendar date advanced. This could be interpreted as support for the hypothesis Rohwer (1986) proposed for female Blue-winged Teals. Acquisition of fat by migrating males would be adaptive because they follow their philopatric mate (Anderson 1985b). Large fat reserves would act as a hedge against unknown migration distances and unknown habitat conditions. Alternatively, a male's use of stored energy to fuel some portion of its breeding activities would presumably lessen constraints on its time budget (Anderson 1984, 1985a, b). Not knowing the reproductive effort of these males makes any conclusion tentative.

*Effect of Canvasback nutrient reserves on reproduction.*—Rohwer's (1986) hypothesis that fat reserves are accumulated primarily for use during spring migration (not reproduction) is supported in male but not female Canvasbacks. Protein and calcium reserves were not related to reproduction with males and provide only small reserves for breeding females.

We reject Rohwer's hypothesis for female Canvasbacks on two lines of evidence. First, fat

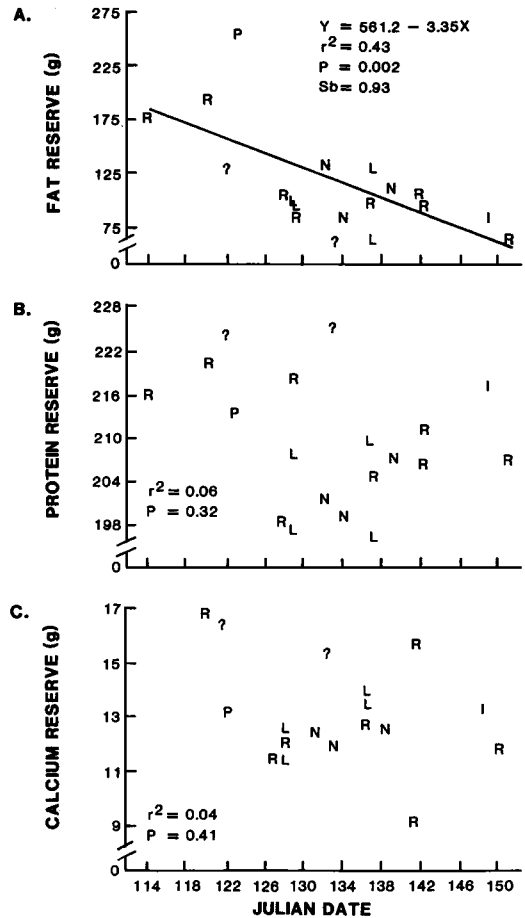


Fig. 5. Regression of fat (A), protein (B), and calcium (C) reserve on Julian date for after-second-year male Canvasbacks. P = pre-rapid follicle growth; R = rapid follicle growth; L = laying; I = incubation; N = renesting, rapid follicle growth; ? = unknown reproductive status.

reserves used by laying females are large enough to account for egg production and a portion of body maintenance. Second, female Canvasbacks increased or at least maintained fat reserves after arrival on breeding areas in both Manitoba (this study) and in Nevada (Noyes and Jarvis 1985). Our data suggest weakly that renesting females use some fat reserves for egg production.

Use of nutrient reserves is significant to breeding Canvasbacks. Females that do not acquire reserves before laying have three options. First, they might abandon nesting altogether. Second, they might initiate rapid follicle growth after arrival and reduce clutch size. Third, they

might delay nest initiation and wait until sufficient reserves are acquired or food availability is adequate. Nest abandonment occurs only during years of severe drought (Stoudt 1982, M. G. Anderson pers. comm.).

Clutch size in temperate nesting ducks appears to be limited by egg viability and predation pressures (Arnold et al. 1987). Still, it is conceivable that the number of eggs laid by Canvasbacks could be reduced from this maximum by lowered nutrient reserves as suggested for other species (e.g. Jones and Ward 1976, Ankney and MacInnes 1978, Drobney and Fredrickson 1985). In Canvasbacks, potential reductions in clutch size by several eggs are comparable to reductions in clutch size caused by Redhead (*Aythya americana*) parasitism (Stoudt 1982). A decrease in clutch size might not be additive to losses from parasitism. If true, a smaller clutch size due to decreased fat reserves would influence reproductive success little.

Fat reserves may have a significant effect on female reproductive success because it influences nest success rather than clutch size. Annual reproductive success of Canvasback and Mallard females is highly dependent upon re-nesting effort (Stoudt 1982, Cowardin et al. 1985). Use of nutrient reserves could allow birds to extend nesting by allowing egg production to occur when food availability is limited (Ryder 1970, Krapu 1981). The probability of a female nesting successfully in a given year would therefore be increased.

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#### LITERATURE CITED

- AFTON, A. D. 1979. Time budget of breeding Northern Shovelers. *Wilson Bull.* 91: 42-49.
- . 1980. Factors affecting incubation rhythms of Northern Shovelers. *Condor* 82: 132-137.
- ALISAUSKAS, R. T., & C. D. ANKNEY. 1985. Nutrient reserves and the energetics of reproduction in American Coots. *Auk* 102: 133-144.
- ANDERSON, M. G. 1984. Parental investment and pair-bond behavior among Canvasback ducks (*Aythya valisineria*, Anatidae). *Behav. Ecol. Sociobiol.* 15: 81-90.
- . 1985a. Variations on monogamy in Canvasbacks (*Aythya valisineria*). Pp. 57-67 in *Avian monogamy* (P. A. Gowaty and D. W. Mock, Eds.). *Ornithol. Monogr.* 37.
- . 1985b. Social behavior of breeding Canvasbacks (*Aythya valisineria*): male and female strategies of reproduction. Ph.D. dissertation, Minneapolis, Univ. Minnesota.
- ANKNEY, C. D. 1984. Nutrient reserve dynamics of breeding and molting Brant. *Auk* 101: 361-370.
- , & A. D. AFTON. 1988. Bioenergetics of breeding Northern Shovelers: diet, nutrient reserves, clutch size, and incubation. *Condor* 90: 459-472.
- , & C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95: 459-471.
- ARNOLD, T. W., F. C. ROHWER, & T. ARMSTRONG. 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. *Am. Nat.* 130: 643-653.
- ASCHOFF, J., & H. POHL. 1970. Rhythmic variations in energy metabolism. *Federation Proc.* 29: 1541-1552.
- BARZEN, J. A. 1989. Patterns of nutrient acquisition in Canvasbacks during spring migration. M.S. thesis, Grand Forks, Univ. North Dakota.
- CALDWELL, P. J., & G. W. CORNWELL. 1975. Incubation behavior and temperatures of the Mallard Duck. *Auk* 92: 706-731.
- CAMPBELL, R. R., & J. F. LEATHERLAND. 1983. Changes in calcium reserves in breeding Lesser Snow Geese (*Chen caerulescens caerulescens*). *Acta Zool. (Stockholm)* 64: 9-14.
- COWARDIN, L. M., D. S. GILMER, & C. W. SHAIFFER. 1985. Mallard recruitment in the environment of North Dakota. *Wildl. Monogr.* 92.
- DOBUSH, G. R. 1986. The accumulation of nutrient reserves and their contribution to reproductive success in the White-winged Scoter. M.S. thesis, Ontario, Univ. Guelph.
- , C. D. ANKNEY, & D. G. KREMENTZ. 1985. The effect of apparatus, extraction time, and solvent

- type of lipid extractions of Snow Geese. *Can. J. Zool.* 63: 1917-1920.
- DONHAM, R. S., C. W. DANE, & D. S. FARNER. 1976. Plasma luteinizing hormone and the development of ovarian follicles after loss of clutch in female Mallards (*Anas platyrhynchos*). *Gen. Comp. Endocrinol.* 29: 152-155.
- DOTY, H. A., D. L. TRAUGER, & J. R. SERIE. 1984. Re-nesting by Canvasbacks in southwestern Manitoba. *J. Wildl. Manage.* 48: 581-584.
- DROBNEY, R. D. 1980. Reproductive bioenergetics of Wood Ducks. *Auk* 97: 480-490.
- . 1982. Body weight and composition changes and adaptations for breeding in Wood Ducks. *Condor* 84: 300-305.
- , & L. H. FREDRICKSON. 1985. Protein acquisition: a proximate factor limiting clutch size in Wood Ducks. *Wildfowl* 36: 122-128.
- FISHER, H. 1967. Nutritional aspects of protein reserves. Pp. 101-124 in *Newer methods of nutritional biochemistry*, vol. 3 (A. A. Albanese and L. A. Orto, Eds.). New York, Academic Press.
- FREED, L. A. 1981. Loss of mass in breeding wrens: stress or adaptation? *Ecology* 62: 1179-1186.
- GATTI, R. C. 1983. Incubation weight loss in the Mallard. *Can. J. Zool.* 61: 565-569.
- GILBERT, A. B. 1971. The ovary. Pp. 1163-1208 in *Physiology and biochemistry of the domestic fowl* (D. J. Bell and B. M. Freeman, Eds.). New York, Academic Press.
- . 1983. Calcium and reproductive function in the hen. *Proc. Nutr. Soc.* 42: 195-212.
- JARVIS, R. L., & J. H. NOYES. 1986. Foods of Canvasbacks and Redheads in Nevada: paired males and ducklings. *J. Wildl. Manage.* 50: 199-203.
- JONES, P. J., & P. WARD. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch size in the Red-billed Quelea *Quelea quelea*. *Ibis* 118: 547-574.
- KENDEIGH, S. C. 1963. Thermodynamics of incubation in the House Wren, *Troglodytes aedon*. *Louisiana, Int. Ornithol. Congr.* 13: 884-904.
- KERR, C. D., C. D. ANKNEY, & J. S. MILLAR. 1982. The effects of drying temperature on extraction of petroleum ether soluble fats of small birds and mammals. *Can. J. Zool.* 60: 470-472.
- KING, J. R., & M. E. MURPHY. 1985. Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? *Am. Zool.* 25: 955-964.
- KRAPU, G. L. 1974. Feeding ecology of Pintail hens during reproduction. *Auk* 91: 278-290.
- . 1981. The role of nutrient reserves in Mallard reproduction. *Auk* 98: 29-38.
- NOYES, J. H., & R. L. JARVIS. 1985. Diet and nutrition of breeding female Redhead and Canvasback ducks in Nevada. *J. Wildl. Manage.* 49: 202-211.
- RANDALL, E. L. 1974. Improved method for fat and oil analysis by a new process of extraction. *J. Assoc. Off. Anal. Chem.* 57: 1165-1168.
- RAVELING, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. *Auk* 96: 234-252.
- REEDNICK, J. 1979. A unique approach to atomic spectroscopy: high energy plasma excitation and high resolution spectrometry. *Am. Lab.* 11(3): 53-61.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pp. 152-297 in *Avian energetics* (R. A. Paynter Jr., Ed.). Cambridge, Massachusetts, Nuttall Ornithol. Club 15.
- ROBBINS, C. T. 1983. *Wildlife feeding and nutrition*. New York, Academic Press.
- ROHWER, F. C. 1986. Adaptive significance of clutch size in waterfowl. Ph.D. dissertation, Philadelphia, Univ. Pennsylvania.
- ROMANOFF, A. L., & A. J. ROMANOFF. 1949. *The avian egg*. New York, Wiley and Sons, Inc.
- RYDER, J. P. 1970. A possible factor in the evolution of clutch size in Ross' Goose. *Wilson Bull.* 82: 5-13.
- SAS INSTITUTE, INC. 1985. *SAS user's guide: statistics*, ver. 5 ed. Cary, North Carolina, SAS Inst.
- SCOTT, M. L. 1973. Nutrition in reproduction—direct effects and predictive functions. Pp. 46-59 in *Breeding biology of birds* (D. S. Farner, Ed.). Washington, D.C., Natl. Acad. Sci.
- SERIE, J. R., D. L. TRAUGER, H. A. DOTY, & D. E. SHARP. 1982. Age-class determination of Canvasbacks. *J. Wildl. Manage.* 46: 894-904.
- SIMKISS, K. 1967. *Calcium in reproductive physiology*. New York, Reinhold Publ. Corp.
- SOKAL, R. R., & F. J. ROHLF. 1981. *Biometry*, 2nd ed. New York, W. H. Freeman and Co.
- STOUDT, J. H. 1982. Habitat use and productivity of Canvasbacks in southwestern Manitoba, 1961-1972. Washington, D.C., U.S. Fish and Wildl. Serv. Spec. Sci. Rep. 248.
- TAKEKAWA, J. Y. 1987. *Energetics of Canvasbacks staging on a Mississippi River pool during fall migration*. Ph.D. dissertation, Ames, Iowa State Univ.
- TOME, M. W. 1984. Changes in nutrient reserves and organ size of female Ruddy Ducks breeding in Manitoba. *Auk* 101: 830-837.
- WELLER, M. W. 1956. A simple field candler for waterfowl eggs. *J. Wildl. Manage.* 20: 111-113.
- . 1957. An automatic nest-trap for waterfowl. *J. Wildl. Manage.* 21: 456-458.
- WYPKEMA, R. C., & C. D. ANKNEY. 1979. Nutrient reserve dynamics of Lesser Snow Geese staging at James Bay, Ontario. *Can. J. Zool.* 57: 213-219.