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NUTRITION OF BREEDING FEMALE RUDDY DUCKS: THE ROLE OF NUTRIENT RESERVES[1]

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Abstract. We determined fat, protein, and mineral content of somatic tissue, and estimated amounts of these nutrients committed to eggs by Ruddy Ducks (*Oxyura jamaicensis*) nesting in southern Manitoba in 1988. Seasonal nutrient dynamics differed between breeding and nonbreeding females. Nonbreeders had less fat and protein reserves than did breeders early in the nesting season, but these then increased and subsequently declined, whereas nutrient reserves of breeders declined linearly with date from the outset of our study. Onset of breeding was related to a nutrient reserve threshold (early RFG [rapid follicle growth] ducks had 22.7 g more fat and 5.1 g more protein than did non-RFG ducks). Adults showed greater propensity to initiate breeding (73% of breeding population) than did yearlings (68% of nonbreeding population), and we relate this to greater fat and protein reserves of adults. Adult breeders had more fat and protein reserves than did yearlings at every stage in the breeding cycle but no age-related differences in use of fat, protein or mineral reserves for clutch formation were found. When controlling for date effects, fat reserves declined ($b = -0.49$) as fat was committed to eggs. Early nesters initiated and ended egg laying with significantly more fat compared to late nesters, although rate of fat use was not different. Protein and mineral reserves were used for clutch formation by early nesters ($b = -0.24$ and -0.08, respectively), but not by late nesters. Among females nearing end of laying, number of developing follicles was related to mineral, but not fat or protein reserves, indicating that mineral reserves were a proximate factor constraining clutch size. Our findings confirm that, for Ruddy Ducks, somatic tissues are important sources of nutrients for clutch formation, and that clutch size is directly related to mineral reserves. Of importance to lifetime reproduction, and thus fitness, is our finding that minimum levels of nutrient reserves appear critical for initiation of breeding by female Ruddy Ducks.

Key words: Clutch size determination; fecundity; nutrient reserves; nutrition; reproduction; Ruddy Ducks; timing of breeding.

INTRODUCTION

Organisms may circumvent resource bottlenecks by buffering shortfalls in energy or nutrient supply through catabolism of nutrient reserves. Somatic tissue can be an important energy source for birds during migration or incubation, or be a source of nutrients for egg production. Lack (1967, 1968) hypothesized that average clutch size in waterfowl (Anseriformes) evolved in relation to average amount of food available to laying females. Ryder (1970) modified this hypothesis to account for greatly reduced feeding by colonial, arctic-nesting Ross' Geese (*Chen rossi*); he hypothesized that clutch size of individual Ross' Geese was proportional to size of energy reserves that each has upon arrival at nesting areas. Ankney and MacInnes (1978) found that potential clutch size in Lesser Snow Geese (*Chen caerulescens*) was related to nutrient reserves, thereby supporting Ryder's ideas for the evolution of clutch size in colonial arctic-nesting geese.

Subsequently, evidence for the role of nutrient reserves in various aspects of reproduction by waterfowl has increased (see Ankney et al. 1991). Ankney and Alisauskas (1991a) reviewed use of nutrient reserves in 16 waterfowl species and found that females in all but one species used lipid reserves for egg production; use of protein and mineral reserves varied and appeared related to differences in foods consumed during egg lay-

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ing versus normal diets during nonbreeding seasons. Regardless, the importance of nutrient reserves for proximate determination of clutch size in waterfowl remains controversial (Ankney et al. 1991, Drobney 1991, Arnold and Rohwer 1991).

Stiff-tailed ducks (Tribe Oxyurini) have the heaviest eggs relative to body mass of all Anatidae (Lack 1968), and a completed clutch may weigh more than the female that laid it. Additionally, Ruddy Ducks (*Oxyura jamaicensis*) lay one egg/day (Siegfried 1976a, Alisauskas and Ankney 1994), which places very high daily demands for nutrients on females producing large clutches. Tome (1984) did not detect significant changes in fat or protein reserves of Ruddy Ducks laying eggs, but his small sample sizes reduced the statistical power of his tests and thus may have led to incorrect conclusions about use of reserves by these ducks. Given the high rate of nutrient demand for egg laying in this species, we were unconvinced specifically about Tome's conclusion that Ruddy Ducks did not show significant reliance on all nutrient reserves for egg production.

Thus, we shot female Ruddy Ducks during the breeding season to more fully understand the role of nutrient reserves in reproduction by these birds. Moreover, we wished to: (1) test our ideas (Alisauskas and Ankney 1992) about thresholds of nutrient reserves for initiation of rapid growth of ovarian follicles (see Ankney and Alisauskas 1991b), (2) compare nutrient reserves in breeders and non-breeders (see Alisauskas et al. 1990), (3) examine seasonal changes in nutrient reserve thresholds (see Reynolds 1972), and (4) analyze the effects of nutrient reserves on terminal clutch size (see Ankney and Afton 1988, Ankney and Alisauskas 1991b). Such an approach is more important than simply considering breeding birds, because factors that affect whether or not a bird breeds in a given year are more important to its fitness than are relatively small-scale variations in clutch size (see Ankney et al. 1991, Arnold and Rohwer 1991).

METHODS

STUDY AREA AND HABITAT CONDITIONS

The study area has been described in some detail by Stoudt (1982). Water levels on wetlands are extremely variable within and among years. From measurements made the first day of each month of May to September, 1985–1991, average water depth of 12 wetlands during our study in May and June 1988 were comparatively high (see Fig. 1 of Arnold 1994); compared to long-term water fluctuations, the last half of the decade was drier than average (1961–1991). Also, nesting effort by Ruddy Ducks during the year of our study was the highest recorded in five years (T. W. Arnold, pers. comm.): 1987 (n = 11 nests found on study area of Arnold [1994]), 1988 (n = 48), 1989 (n = 0), 1990 (n = 11), and 1991 (n = 9); search effort was greater in years with fewer nests. In general, conditions for nesting by Ruddy Ducks were very good in 1988, and probably about average when considered over a longer term.

FIELD COLLECTIONS

Ninety-seven female Ruddy Ducks were shot (under permit from Canadian Wildlife Service) on wetlands within 50 km of Minnedosa, Manitoba in 1988. We were especially interested in sampling birds in the phase of rapid follicle growth (RFG); therefore, our sampling effort reflected our success at acquiring birds in RFG. After retrieval, we weighed birds (10 g) and immediately injected 70% ethanol into esophagi to prevent post-mortem digestion (Swanson and Bartonek 1970). At day's end, we removed esophageal and proventricular contents and placed them in labelled containers with additional 70% ethanol. Also, after cutting through the ribcage dorsally, we removed the ovary, oviduct and oviducal egg, if present. After counting postovulatory follicles (N_{POF}) we placed reproductive tissue in 10% formalin. Carcasses were then labelled, sealed in plastic bags, and frozen.

CARCASS ANALYSIS

Dissections. After thawing specimens, we took seven measurements using dial calipers: *bill width* (0.1 mm)—widest dimension of ramphotheca, *bill height* (0.1 mm)—greatest dorsoventral dimension of ramphotheca, *culmen* (0.1 mm)—distance from anterior tip of bill to feather line, *tarsus* (0.1 mm)—from distal point of foot bent toward body, to notch at ankle, *head length* (0.1 mm)—greatest anterior-posterior dimension of head, *head width* (0.1 mm)—widest lateral dimension of head, and *middle toe* (0.1 mm)—distance from base of nail to junction of toe with tarsus. We took three measurements with a flat ruler: *wing chord* (1 mm)—distance from wrist of bent wing to most distal point of primary feathers, *wing length* (1 mm)—distance from junction of wing and body to most distal point of primary feathers (with wing flattened and perpendicular to the vertebral column), and *total length* (1 mm)—distance from anterior tip of bill to most posterior point of rectrices with bird laid flat. We took two internal measurements with calipers after removal of skin and feathers: *keel* (0.1 mm)—distance along median line from anterior notch to posterior point of sternum, and *body length* (0.1 mm) from joint behind last cervical vertebra to joint anterior to first mobile caudal vertebra.

One half of the breast (*pectoralis* and *supracoracoideus*) muscle and muscles of one leg were removed and weighed (0.1 g) separately. The alimentary tract from junction of proventriculus and gizzard to cloaca was excised. Fat depots around neck and abdomen were removed, weighed (0.1 g) separately and discarded. Intestines were uncoiled and pancreas was removed and weighed (0.1 g). Lengths of small intestine (1 mm), large intestine (1 mm) and both caeca together were each measured with a flat steel ruler; the bursa of Fabricius was measured (1 mm), if present. Ruddy Ducks were called "adult" if no bursa was present (Hochbaum 1942), and "yearling" if one was present ($\bar{x}$ = 14.0 mm ± 4.5 SD, range 6–21). Gizzard, small intestine, large intestine and caeca were separated from one another with a scalpel, stripped of visible fat depots, and weighed (0.1 g); each was then opened, contents were discarded, and, after rinsing with water and patting dry with paper towels, reweighed (0.1 g). Heart and liver were weighed (0.1 g) separately. Breast muscles, leg muscles, and liver were each dried to constant mass at 80°C. All other organs (except fat depots) were combined with the carcass (including feathers, except remiges and rectrices which are difficult to grind because of large keratinous shafts); the carcass was then homogenized by passing through a food processor at least three times and mixing thoroughly after each grind.

Somatic nutrients. Determinations of fat, protein, and ash were made using techniques described by Ankney and Afton (1988). From these determinations, and using S_{ash} = total somatic ash, we calculated, for each bird, total somatic fat (S_{fat}):

$$S_{fat} = F_{carcass} + F_{abdomen} + F_{neck} + F_{leg} + F_{breast} + F_{liver},$$

and total somatic protein ($S_{protein}$):

$$S_{protein} = L_{carcass} - S_{ash} + L_{leg} + L_{breast} + L_{liver}.$$

where L is lean dry mass and F is fat in each body component.

CLUTCH NUTRIENTS

Egg composition data for Ruddy Ducks and details about laboratory analysis necessary for estimating clutch nutrients committed by each female in our sample were given by Alisauskas and Ankney (1994). Fat invested in clutch formation by each duck (R_{fat}) was estimated following

$$R_{fat} = \Sigma F_{fol} + \bar{F}_{yolk}(N_{POF}) + F_{ovary}$$

where F_{fol} was fat in each enlarged follicle, $\bar{F}_{yolk}$ was a constant (9.18 g) equal to average fat/egg (n = 12 eggs), N_{POF} was number of ovulated follicles, and F_{ovary} was fat in remaining ovary tissue. If a duck had an egg in the oviduct, we used the fat mass of that egg for $\bar{F}_{yolk}$ (only 13 ducks had oviducal eggs for which egg fat could be determined).

Protein production associated with clutch formation ($R_{protein}$) was estimated as

$$R_{protein} = \Sigma L_{fol} + L_{ovary} + L_{ovid} + N_{POF}(\bar{L}_{yolk} + \bar{L}_{albumen})$$

where L_{fol}, L_{ovary}, and L_{ovid} are the lean dry mass of each follicle, remainder of ovary, and oviduct in each female, and $\bar{L}_{yolk}$ and $\bar{L}_{albumen}$ are the average lean dry fractions of yolk (4.77 g) and albumen (4.59 g) per egg (n = 12 eggs). When available from oviducal eggs (n = 13), we used lean dry fractions of egg yolk plus dry albumen from such eggs for $\bar{L}_{yolk}$ and $\bar{L}_{albumen}$, respectively.

Minerals in the clutch, R_{ash}, were estimated by

$$R_{ash} = N_{POF}\bar{M}_{egg}$$

where $\bar{M}_{egg}$ = mean mass of eggshell, 6.80 g.

We assigned each bird a reproductive status according to state of reproductive organs or presence of a brood patch.

(*A*) *BREEDERS* included RFG Ruddy Ducks (those with rapid follicle growth) which could be either *prelayers* (n = 32; contained ≥1 yolky and rapidly developing ovarian follicles, and no atretic or ovulated follicles), or *layers* (n = 26; contained ≥1 rapidly developing follicle and ≥1 ovulated follicle); *early prelayers* (n = 15) were a subcategory of prelayers and were those with ≤2 g ovarian fat (Fig. 1); *late layers* (n = 28), a subcategory of *layers* and *early incubation*, contained ≤5 rap-

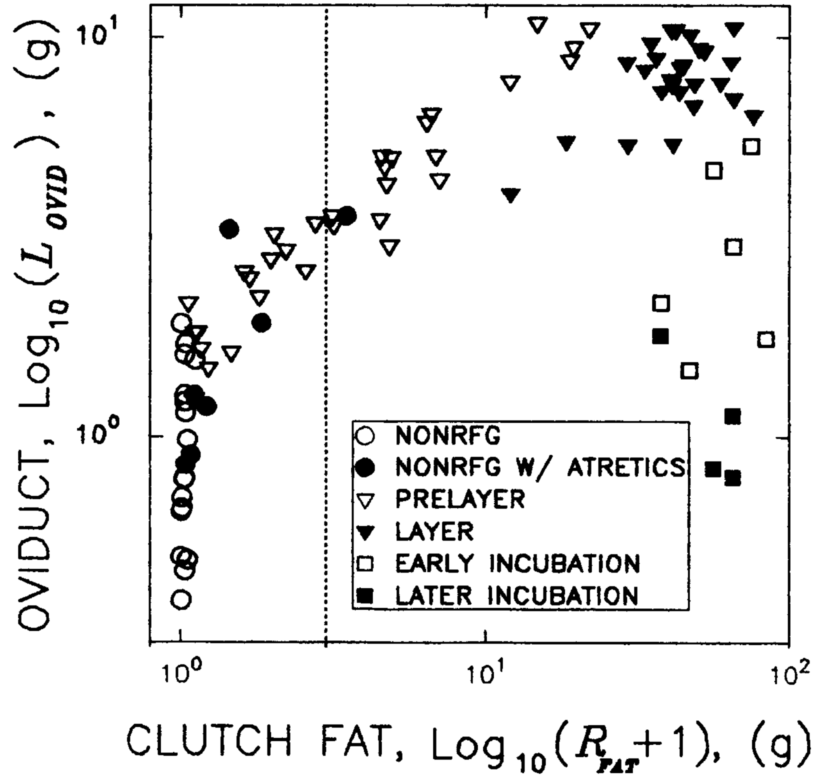

FIGURE 1. Relation between dry oviduct mass and clutch fat for Ruddy Ducks in various stages of breeding and nonbreeding as defined in METHODS. Early prelayers are prelayers with less than 2 g of clutch fat (represented by vertical dotted line).

idly developing follicles and ≥ 1 ovulated follicle. Ruddy Ducks were in *early incubation* (n = 7) if they had no developing follicles, but had a brood patch and enlarged (≥ 10 g wet mass) oviduct; those in *later incubation* (n = 5) had no developing follicles, but had a brood patch and a regressed (< 10 g wet mass) oviduct (Fig. 1).

We also classified a single female as a renester because it had developing follicles, very small POFs (similar to those of a duck in later incubation) and a brood patch. This bird was omitted from any further analyses.

(*B*) *NONBREEDERS* (n = 26) included all other birds, i.e., those without enlarged oviducts, or ovulated follicles, or rapidly developing follicles, or brood patches, and seven ducks that had somewhat enlarged oviducts but contained only atretic and no developing follicles and no POFs (Fig. 1). NONBREEDER is synonymous, in this paper, with NONRFG birds, the appropriate usage depending on specific comparisons and analyses reported.

STATISTICAL ANALYSES

Structural size correction. We used only some structural measurements to scale variation in S_{fat}, $S_{protein}$ and S_{ash} due to body size (Alisauskas and Ankney 1987). First, using MANOVA, we confirmed that there were no overall morphometric differences between breeders and nonbreeders (F = 0.65; 12, 48 df; P = 0.79), nor between early prelayers and NONRFG birds (F = 0.42; 12, 9 df; P = 0.92). We conducted principal components analysis (PCA) of morphological measurements using both correlation and covariance matrices. Because morphological structures of some specimens were damaged during collection, this resulted in substantial missing data when all 12 measurements were used in PCA. Therefore, we repeated PCA after systematically deleting morphological variables with the greatest missing data. Correlations between scores from each first principal component, and somatic fat, protein and mineral fractions were compared to determine the best correction for structural size while retaining the largest sample size of birds. We selected a principal component derived from a correlation matrix of wing chord and body length (loadings 0.71, 0.71, respectively, accounting for 59% of total variation) because 92 of 97 ducks had both measurements recorded, and because it was correlated with each somatic nutrient, and was generally better correlated with these than were univariate measurements. We used least-squares regression of S_{fat}, $S_{protein}$, and S_{ash} on this size index (PC_{2cor}) and found:

$$S_{fat} = 84.39 + 7.233PC_{2cor},$$

$$df = 90, \quad r^2 = 0.04, \quad P < 0.05,$$

$$S_{protein} = 124.4 + 3.979PC_{2cor},$$

$$df = 90, \quad r^2 = 0.19, \quad P < 0.0001,$$

$$S_{ash} = 19.66 + 0.958PC_{2cor},$$

$$df = 90, \quad r^2 = 0.14, \quad P < 0.0001.$$

We used the residual (observed − predicted) values from these regressions to calculate new values (y_i) for each observation corrected for structural size:

$$y_i = y_{obs} - [a + b(PC_{2cor})] + \bar{Y}_{obs}.$$

These size-corrected values of S_{fat}, $S_{protein}$, and S_{ash} were used in subsequent analyses. Where this resulted in missing data ($n = 5$ females) due to missing morphological measurements, data uncorrected for size were used.

We tested for changes in mean length of bursa of Fabricius among yearlings using one-way analyses of variance (ANOVA) across reproductive categories (PROC GLM, SAS 1990).

We tested the hypothesis that initiation of clutch formation was related to nutrient reserve status of Ruddy Duck females by comparing nutrient reserves of NONRFG females with those of early prelayers; we used early prelayers to control for variation in depletion of reserves following initiation of follicle growth. Collection date and age were included in a saturated model (PROC GLM, SAS 1990).

To analyze relations between nutrient investment in eggs and respective somatic nutrients, we used a general linear model (PROC GLM, SAS 1990), and analysis of covariance (ANCOVA) of somatic nutrient with respect to clutch nutrient, female age, date of first ovulation (i.e., date of collection minus number of ovulated follicles) and all interactions. We used date of first ovulation to separate any date effects from any effects of commitment to clutch nutrients on nutrient reserves.

For each of the two preceding analyses, we followed the protocol used by Ankney and Alisauskas (1991b). If overall models were significant ($P < 0.05$), we removed non-significant three-way interactions from the model ($P > 0.10$), and analyses were redone. If following this second analysis, two-way interactions were non-significant ($P > 0.10$), they were deleted from the model and the analysis was repeated using only main effects as predictors in the model. Unlike Ankney and Alisauskas (1991b), we carried these analyses a step further and any non-significant ($P > 0.10$) main effects were removed from the model before a final analysis was done. Type III sums of squares were used for determining P values in all analyses.

To illustrate graphically any influence of first ovulation date on effect of clutch nutrients on respective somatic nutrients, we coded RFG birds as "EARLY" if they were collected on or before 12 June ($n = 26$), and "LATE" if after 12 June ($n = 35$). This was near the mean nest initiation date (11 June, see below); this also was the date before and after which the most similar sample sizes could be assigned to each group, while maintaining at least a 10 day range in each. We used linear regression (PROC REG, SAS 1990) between somatic nutrients and clutch nutrients for EARLY and LATE layers separately to further examine details of changes in slopes or intercepts with season.

To determine whether number of developing follicles was correlated with nutrient reserves in late layers with $N_{POF} < 6$ (Ankney and Afton 1988), we first regressed (PROC GLM, SAS 1990) each nutrient reserve against N_{POF}. We tested significance of correlations between each set of residuals representing fat, protein and mineral reserves with number of developing follicles using *a priori*, one-tailed tests.

RESULTS

GENERAL BREEDING CHRONOLOGY

In 1988, the first Ruddy Duck was observed on the study area on 25 April (Fig. 2) during a standardized roadside census of 68 wetlands (T. W. Arnold, pers. comm.). The earliest known initiation date for 26 nests found on the study area

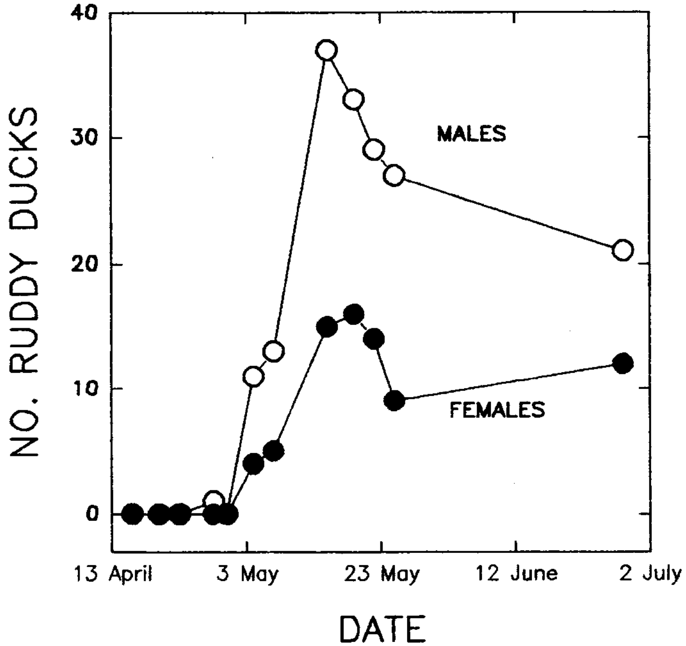

FIGURE 2. Arrival phenology of Ruddy Ducks as determined from standardized censuses of 68 wetlands near Minnedosa, Manitoba, 1988 (T. W. Arnold, pers. comm.).

was 26 May, and the latest was 21 June ($\bar{x}$ = 11 June ± 9 days [SD]). Based on 22 nests with available data, clutch size (CS, $\bar{x}$ = 6.0 ± 1.1 [SD]) declined with date (d, May 25 = day 1) as $CS = 8.85 - 0.13\ d$ ($F = 8.00$, $r^2 = 0.25$, $P = 0.01$).

VARIATION IN NUTRIENT RESERVES BY STATUS AND AGE

Adult Ruddy Ducks had more body fat and protein, but not more mineral, than did yearlings (Table 1). These differences were consistent across all stages of breeding as shown by lack of interaction between age and status for each dependent variable. We repeated the analyses after removing variation due to Julian date of collection and found the same patterns (Table 1).

Yearlings comprised a decreasing proportion in samples organized chronologically by reproductive status: 68% for NONRFG, 34% for prelayers, 25% for layers, 14% of early incubators and 0% of later incubators. This decline ($r_s = -1.0$, $n = 5$, $P = 0.05$) may have been an artifact of later nesting by yearlings vs. adults. If a large proportion of yearlings initiated reproduction after 28 June, the last date of collection in our study, then yearlings would have been undersampled. However, because nest initiation dates ranged from 26 May until 21 June for nests found on census routes (T. W. Arnold, pers. comm.), it is likely that most nest initiations had already taken place before our last collection date. A second possibility is that yearlings became underrepresented in sequential stages of reproduction because their success at completing each stage is proportionally lower than that of adults. There was no difference in collection dates between ages (2-way ANOVA: $F = 1.02$, df = 1, 64, $P = 0.32$) when controlling for breeding status. Among ducks showing RFG, mean initiation date for adults was 15 June compared to 16 June for yearlings ($F = 0.83$, df = 1, 69, $P = 0.37$) thereby ruling out the first explanation while supporting the second. A final explanation for decreasing representation by yearlings in progressively later nesting categories is that the bursa of Fabricius, which we used to age Ruddy Ducks, regresses in yearlings as they attempt reproduction. We found no evidence of decline in bursa length ($F = 0.25$, df = 3, 34, $P = 0.86$) among nonbreeding, prelaying, laying or incubating yearling Ruddy Ducks.

TABLE 1. Relation between nutrient reserves ($\bar{x} \pm 1$ SE), age (Ad = Adult, Yr = Yearling), and stage of the breeding season of Ruddy Ducks collected in southern Manitoba, May–June, 1988. Sample sizes in parentheses.

		Stage in breeding season[a]					Effect[b]		Effect scaled for date[c]	
Variable	Age	NONRFG	Pre-laying	Laying	Early Inc.	Later Inc.	Stage	Age	Stage	Age
Body mass[d]	Ad	588.1 ± 18.6[e] (9)	646.2 ± 12.2 (21)	614.4 ± 12.5 (20)	590.9 ± 22.8 (6)	576.5 ± 24.9 (5)	0.0001	0.0001	0.0001	0.0003
	Yr	532.3 ± 13.5 (17)	610.7 ± 16.8 (11)	558.9 ± 22.8 (6)	484.7 ± – (1)	–				
Body fat[f]	Ad	92.2 ± 10.5 (9)	111.3 ± 6.9 (21)	87.0 ± 7.0 (20)	77.3 ± 12.9 (6)	53.9 ± 14.1 (5)	0.0001	0.0041	0.0011	0.0073
	Yr	64.3 ± 7.6 (17)	99.8 ± 9.5 (11)	59.2 ± 12.9 (6)	54.2 ± – (1)	–				
Body protein[f]	Ad	127.6 ± 2.6 (9)	131.0 ± 1.7 (21)	125.0 ± 1.8 (20)	120.1 ± 3.2 (6)	123.7 ± 3.6 (4)	0.0022	0.0063	0.0058	0.0079
	Yr	118.4 ± 1.9 (17)	127.1 ± 2.4 (11)	122.6 ± 3.2 (6)	118.1 ± – (1)	–				
Body ash[f]	Ad	20.4 ± 0.8 (9)	20.7 ± 0.5 (21)	19.6 ± 0.5 (20)	19.1 ± 1.0 (6)	18.4 ± 1.1 (5)	NS	NS	NS	NS
	Yr	18.5 ± 0.6 (17)	20.4 ± 0.7 (11)	20.3 ± 1.0 (6)	19.6 ± – (1)	–				

[a] See Methods for definitions.

[b] No interactions were significant, so data were reanalyzed using only main effects in the model.

[c] Same analysis as [b], except that variation due to calendar date was removed beforehand, converting $S_{ij} = S_{i,obs} - [a + b\,(date)] + \bar{S}_i$, where i = *body mass, fat protein* or *mineral,* and j refers to individual Ruddy Ducks.

[d] Excluding esophageal contents.

[e] Standard error as computed using LSMEANS option in PROC GLM (SAS 1990).

[f] Variables scaled to structural body size — see Methods.

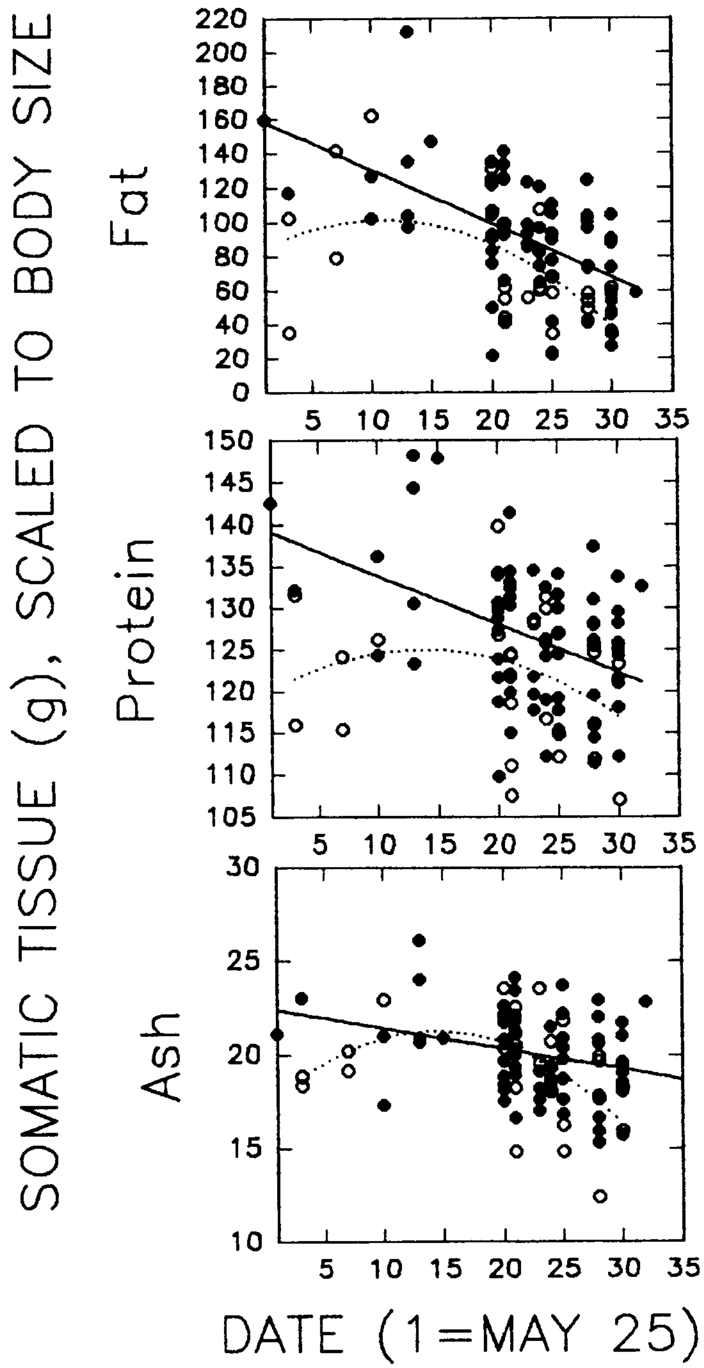

FIGURE 3. Scatterplot of somatic (A) fat, (B) protein and (C) minerals in breeding (solid symbols and lines) and nonbreeding (open symbols, dotted lines) female Ruddy Ducks. Shown for each group (breeders vs. nonbreeders) are models (linear vs. quadratic) that best fit data.

TABLE 2. Comparison of linear and quadratic models fitted to somatic fat, protein and mineral against calendar date (1 = 25 May 1988).

Somatic tissue scaled to body size	Nonbreeding				Breeding			
	Linear		Quadratic		Linear		Quadratic	
	r^2	P	R^2	P	r^2	P	R^2	P
Fat	0.16	0.024	0.22	0.023	0.29	0.0001	0.29	0.0001
Protein	0.00	0.460	0.00	0.427	0.17	0.0003	0.16	0.0011
Mineral	0.02	0.230	0.17	0.045	0.08	0.011	0.06	0.041

VARIATION WITH DATE

Dynamics of nutrient reserves of breeding Ruddy Ducks differed from those that had not as yet shown signs of breeding (Fig. 3). Linear models of nutrient reserves with date fit the data better for breeders, whereas quadratic models fit the data better for nonbreeders, judging from higher coefficients of determination (Table 2). Data for nonbreeders suggested storage of somatic fat, protein and mineral reserves shortly after our collections began. Breeders, on the other hand, did not store nutrients after collections began, but had more nutrient reserves than did nonbreeders (Fig. 3, see below). It is not known whether some Ruddy Ducks classified as nonbreeders would have become breeders had they been collected some days later.

THRESHOLD FOR INITIATION OF RFG

The ratio of yearling ($n = 17$) to adult ($n = 9$) NONRFG birds was higher than the ratio of yearlings ($n = 4$) to adults ($n = 11$) in early RFG ducks (likelihood ratio $G = 5.7$, df = 1, $P = 0.017$). Similarly, the ratio of breeding (51) to nonbreeding (8) adults (86%; includes all categories from NONRFG through incubation) was greater than the ratio of breeding (18) to nonbreeding (17) yearlings (49%; likelihood ratio $G = 13.6$, df = 1, $P < 0.001$).

The propensity for female Ruddy Ducks to attempt to breed was related not only to age, but also to size of nutrient reserves. Adults had higher levels of somatic fat, protein and mineral than did yearlings (Table 3). Controlling for age and date of collection, early prelayers had 22.7 g more fat and 5.14 g more protein than did NONRFG birds (Fig. 4, Table 3), but no differences were evident in mineral reserves (Table 3). No interaction existed between size of reserves and proclivity to breed versus age (Table 3).

ROLE OF NUTRIENT RESERVES IN CLUTCH FORMATION

We used regression analyses to determine rates of decline in nutrient reserves relative to amount of respective nutrients invested in eggs (Table 4, Figs. 5–7). Consistent with data in Figure 3, fat reserves declined with calendar date ($b = -2.14$ g/d) in female Ruddy Ducks during RFG. Independent and additive to this was a significant effect of egg fat commitment with −0.49 g decline in fat reserve for every gram of egg fat committed (Table 4). Thus taken together, these two

TABLE 3. Equations from general linear model (SAS 1990) based on least-squares regression with Type III sums of squares relating somatic nutrients of 41 female Ruddy Ducks to reproductive status (nonbreeder = 0, early-RFG = 1), age (yearling = 0, adult = 1) and collection date. Values in parentheses are 1 SE.

Dependent variable[a]	Model			Intercept	Source[b]	Estimate	F	P[c]
	F	P	R^2					
S_{fat}	9.93	0.0001	0.45	98.87 (11.51)	Rep. Status	22.7 (9.21)	6.06	0.0186
					Age	18.01 (8.95)	4.05	0.0514
					Date[d]	−1.50 (0.50)	9.07	0.0047
$S_{protein}$	10.67	0.0002	0.36	118.69 (2.13)	Rep. Status	5.14 (2.72)	3.57	0.0665
					Age	8.41 (2.62)	10.29	0.0027
S_{ash}	9.25	0.0042	0.19	18.55 (0.54)	Age	2.36 (0.78)	9.25	0.0042

[a] Corrected for variation due to body size (see Methods).
[b] Nonsignificant ($P > 0.10$) 3-way and 2-way interactions and main effects excluded from model (see Methods).
[c] Probability that the slope = 0.
[d] Date = collection date where 1 = 25 May.

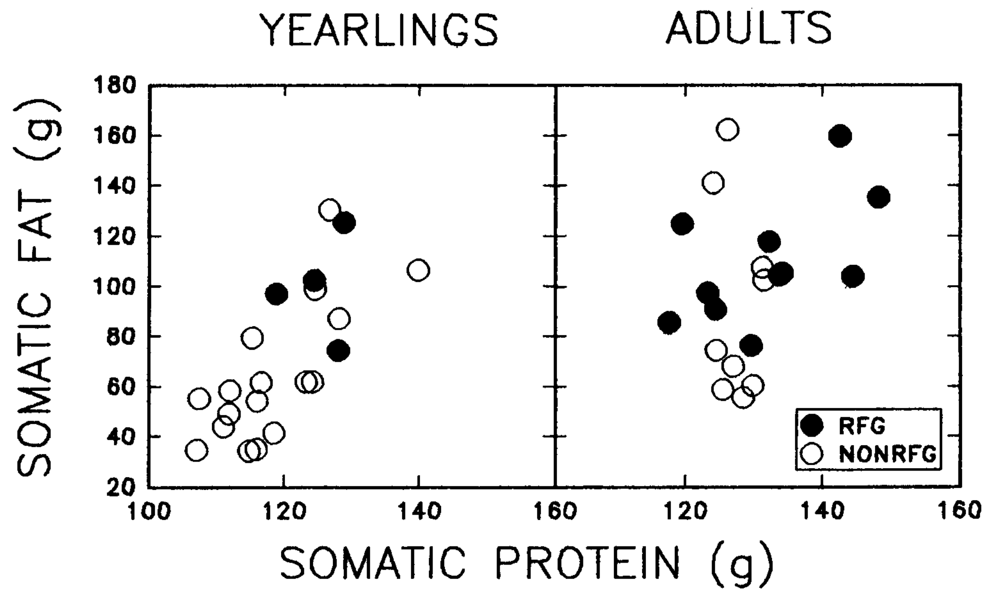

FIGURE 4. Relation between fat and protein reserves of nonbreeding (NONRFG) female Ruddy Ducks with early prelayers (see METHODS).

findings show that, although early nesters and late nesters had similar slopes (−0.50 vs. −0.54, respectively, Fig. 5), early nesters began laying cycles with significantly more fat reserve (114.4 g) than did late nesters (97.3 g). Age did not influence size of initial fat reserves, or fat loss with date or with egg fat commitment.

Somatic protein was significantly negatively related to date of first ovulation ($b = -0.68$ g/d) and to protein commitments to eggs ($b = -0.41$ g/g) in the overall model (Table 4), but a significant ($P = 0.0657$) interaction between these two main effects rendered these estimates unstable. The relation between somatic protein and clutch protein was significant ($b = -0.24$ g/g) in EARLY ducks, but not ($b = -0.004$ g/g) in LATE ducks (Fig. 6). Similar to fat relationships, however, the intercept (135.5 ± 5.2, 95% CI) for EARLY birds was significantly higher than for LATE birds (125.0 ± 3.8, 95% CI). Age did not

TABLE 4. Equations from general linear model (SAS 1990) based on least-squares regression with Type III sums of squares relating somatic nutrients (Y) of 61 female Ruddy Ducks versus their commitment to clutch nutrients, date of first ovulation and age (yearling = 0, adult = 1). Values in parentheses are 1 SE.

Dependent variable[a]	Model			Intercept	Source[b]	Estimate	F	P[c]
	F	P	R^2					
S_{fat}	13.08	0.0001	0.31	146.07 (12.10)	R_{fat}	−0.49 (0.15)	11.63	0.0012
					Date[d]	−2.14 (0.56)	14.52	0.0003
$S_{protein}$	4.97	0.0039	0.21	142.34 (4.44)	$R_{protein}$	−0.41 (0.18)	5.25	0.0257
					Date	−0.68 (0.21)	10.19	0.0023
					$R_{protein}$ × Date	0.02 (0.01)	3.52	0.0657
S_{ash}	3.01	0.0181	0.22	18.93 (1.99)	$R_{mineral}$	−0.16 (0.08)	4.45	0.0394
					Age	−4.80 (2.27)	4.48	0.0389
					Date (Adults)	−0.17 (0.06)	9.12	0.0038
					Date (Yearlings)	0.07 (0.09)	0.62	0.4329
					$R_{mineral}$ × Date	0.007 (0.004)	2.80	0.0998

[a] Corrected for variation due to body size (see Methods).
[b] Nonsignificant ($P > 0.10$) 3-way and 2-way interactions and main effects excluded from model (see Methods).
[c] Probability that the slope = 0.
[d] Date of first ovulation = collection date − n_{POF} where on 25 May, collection date = 1.

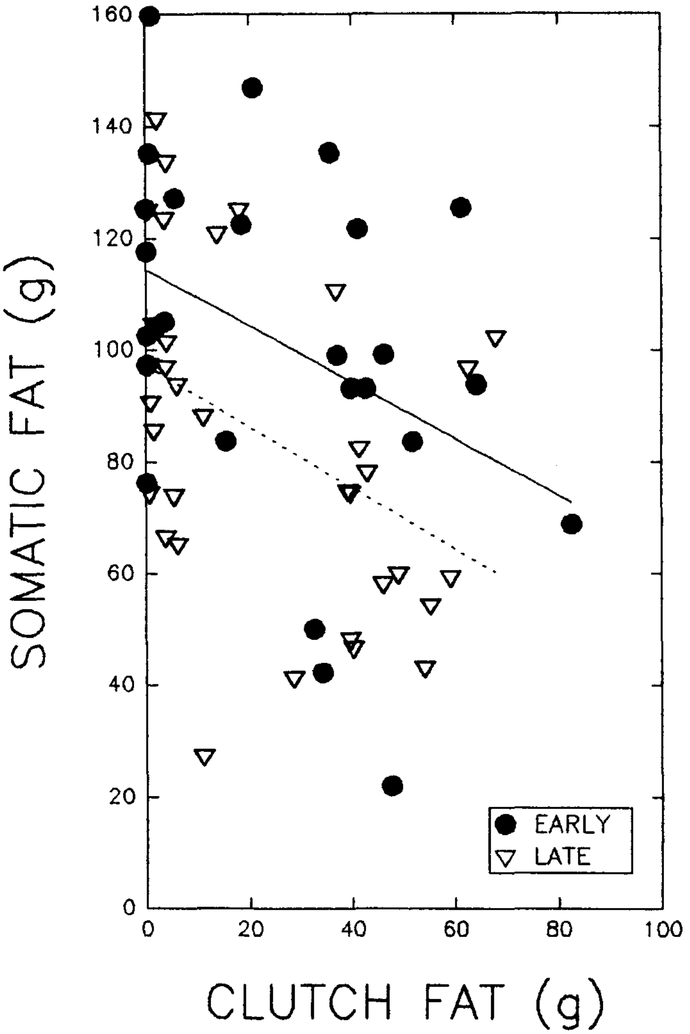

FIGURE 5. Relation of fat reserves (S_{fat}) in female Ruddy Ducks to their commitment to clutch fat (R_{fat}). EARLY ducks ($S_{fat} = 114.44 - 0.50\ R_{fat}$, $r^2 = 0.11$, $P = 0.0537$) had dates of first ovulation from 24 May to 12 June 1988, and LATE ducks ($S_{fat} = 97.33 - 0.54\ R_{fat}$, $r^2 = 0.16$, $P = 0.0102$) from 13 June to 22 June 1988.

influence initial protein level, or protein loss with date or with egg protein commitment (Table 4).

Mineral reserves declined with commitment to eggshell formation ($b = -0.16$ g/g); however, as with clutch protein, clutch eggshell interacted significantly with date of first ovulation (Table 4) in affecting somatic mineral levels; ignoring age effects, mineral reserves in EARLY ducks declined 0.08 g for every gram of eggshell produced, whereas no significant relationship existed among LATE Ruddy Ducks (Fig. 7). Independent of any effect of eggshell production, somatic mineral declined significantly with date in adults ($b = -0.17$ g/d), but not in yearlings (Table 4).

Generally, relations between somatic nutrients and respective clutch nutrients were not strong in significant regressions done separately for EARLY and LATE ducks; coefficients of variation calculated for fat, protein, and mineral reserves were only 16%, 31% and 27%, respectively, in each model (Figs. 5–7).

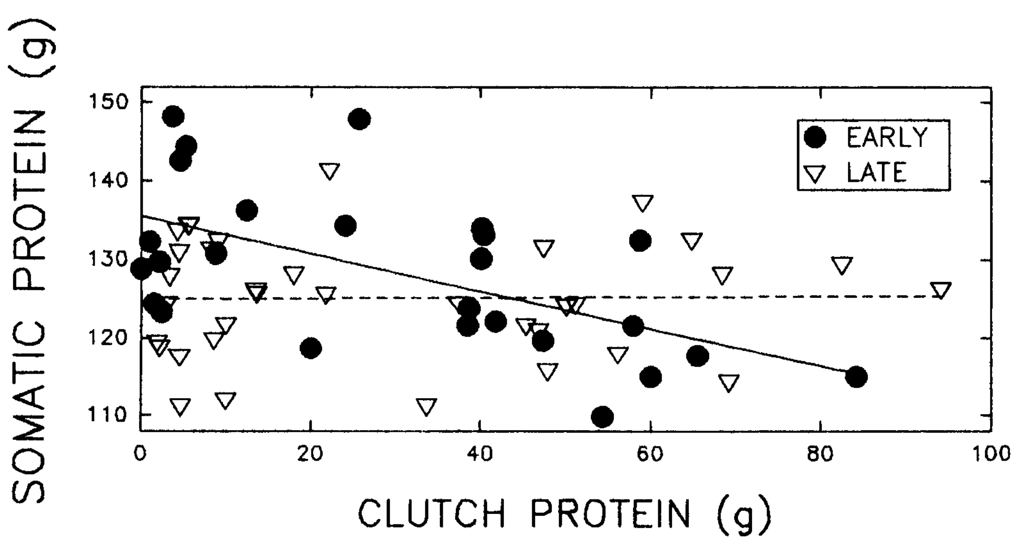

FIGURE 6. Relation of somatic protein ($S_{protein}$) in female Ruddy Ducks to their commitment of clutch proteins ($R_{protein}$). EARLY ducks ($S_{protein} = 135.52 - 0.24\ R_{protein}$, $r^2 = 0.31$, $P = 0.0020$) had dates of first ovulation from 24 May to 12 June 1988, and LATE ducks ($S_{protein} = 125.01 - 0.004\ R_{protein}$, $r^2 = 0.03$, $P = 0.9347$) from 13 June to 22 June 1988.

THRESHOLD FOR TERMINATION OF RFG

Number of developing follicles was not correlated with either somatic fat ($r = -0.21$, $P = 0.288$) or protein ($r = 0.05$, $P = 0.813$), but was correlated ($r = 0.34$, $P = 0.074$, one-tailed test) with amount of somatic mineral (Fig. 8), after accounting for variation in nutrient reserves due to number of ovulated follicles.

DISCUSSION

Maximum daily costs of egg production by Ruddy Ducks, as a percentage of BMR (279%), are among the highest of all waterfowl (Alisauskas and Ankney 1992, 1994). How do Ruddy Ducks supply nutrients at a rate sufficient to meet these very high costs? Why do Ruddy Ducks not prorate costs over a longer period, e.g., by lowering

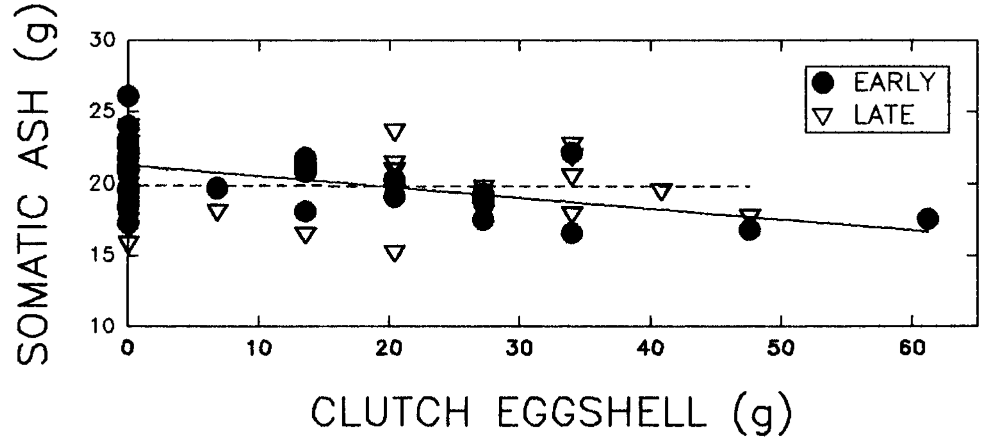

FIGURE 7. Relation of somatic ash content (S_{ash}) of female Ruddy Ducks to their eggshell production ($R_{mineral}$). EARLY ducks ($S_{ash} = 21.28 - 0.08\ R_{mineral}$, $r^2 = 0.27$, $P = 0.0039$) had dates of first ovulation from 24 May to 12 June 1988, and LATE ducks ($S_{ash} = 19.87 - 0.0007\ R_{mineral}$, $r^2 = 0.03$, $P = 0.9779$) from 13 June to 22 June 1988.

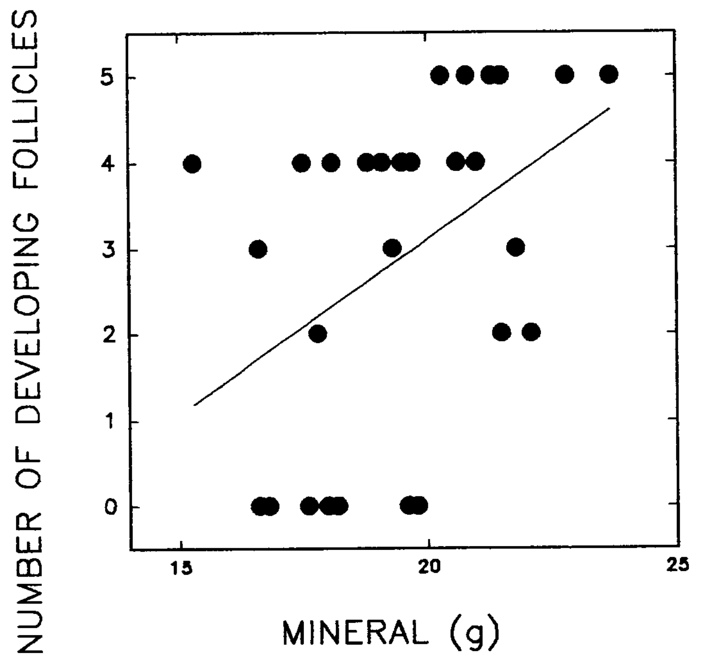

FIGURE 8. Relation between somatic ash and number of developing follicles in Ruddy Ducks with >0 ovulated follicles and <6 developing follicles.

laying rates, to offset daily costs? We believe that answers to these questions lay in a critical interplay between use of nutrient reserves and selection of wetlands with abundant food that is prerequisite to a strategy of extreme rates of nutrient supply to eggs.

Tome (1984) compared mean nutrient reserves of Ruddy Ducks in groups similar to ours (Table 1), and found that endogenous fat and protein were not used significantly for egg production, but that endogenous minerals were used to form eggshells. Tome (1984:830) concluded that Ruddy Ducks "depend almost exclusively upon dietary intake to meet the energy and nutrient requirements of reproduction". We are unsure if his failure to document use of fat and protein reserves resulted from small sample size of Ruddy Ducks in RFG ($n = 15$), or from his statistical approach (see Alisauskas and Ankney 1992 for a comparison and discussion), but we suspect that 15 RFG birds were inadequate to test the hypothesis of no relation between nutrient reserves and nutrient commitment to eggs. Some of this discrepancy may arise from different years of study. Regardless, with a sample of 61 RFG birds, we found a complex relationship between use of somatic tissue for clutch nutrients and date. About 49% of fat, about 24% of protein and 8% of minerals in eggs were supplied by nutrient reserves in early nesters, but late nesters relied completely on exogenous protein and mineral while still supplying about half of their clutch fat with fat reserves (Table 4). The contribution of somatic mineral is not trivial, given the high daily rates of nutrient demand for egg production, and these reserves may be critical in covering daily mineral deficits of laying Ruddy Ducks.

Coefficients of determination for regressions of fat, protein and mineral reserves on their respective clutch nutrients were comparatively low ($r^2 \leq 0.31$, Figs. 5–7) even when significant. We think that both methodological and ecological processes may have confounded these relations. Alisauskas and Ankney (1992) cautioned that use of species-specific averages for egg composition entails measurement error in the independent variable, i.e., egg nutrient commitment. For example, mean yolk lipid determined from 12 Ruddy Ducks was 9.18 g and ranged from 7.86 g to 10.51 g (Alisauskas and Ankney 1994). For a female that laid seven eggs, we estimated that

64.3 g of egg lipid was produced using average yolk lipid, but using minimum or maximum values, the estimate becomes 55.0 g or 73.6 g, respectively, a difference of 34%. A useful test of the magnitude of error could be done with species (such as non-parasitic hole-nesters whose nests are easier to find and monitor) for which nutrient composition of entire clutches could be assigned to females that produced them. Coefficients of determination for regressions of nutrient reserves on egg nutrients using species-specific averages for egg composition vs. female-specific egg composition then could be compared. Only 13 ducks in our sample had undamaged oviducal eggs so we could not properly evaluate the effect of using a species average of egg composition rather than female-specific values of egg nutrients.

ROLE OF EXOGENOUS NUTRIENTS IN EGG FORMATION

High unexplained variation in nutrient reserves of laying Ruddy Ducks also may stem from a combination of ecological factors: inter-female variation in nutrient reserves at the start of laying and/or inter-female variation in assimilation of exogenous nutrients, exacerbated by variation in food availability and efficiency of prey intake.

The importance of feeding during egg-laying by Ruddy Ducks is clear (Tome 1991). Their main foods are benthic invertebrates, primarily Chironomidae (Siegfried 1973; Woodin and Swanson 1989; Alisauskas and Ankney, unpubl. data) which may be difficult to locate and more costly to obtain compared to prey exploited by other duck species. First, to obtain them, birds must dive and strain them from the soft bottom of a wetland basin. The difficulty is compounded for Ruddy Ducks because they forage using tactile rather than visual cues (Tome and Wrubleski 1988). Second, chironomid larvae are patchily distributed and there is great variation in larval density among patches (Gray 1980, Tome 1991). Third, patches are temporally variable because of asynchronous maturation of larvae among patches (Tome 1988). Disappearance of a chironomid patch, through either depletion by Ruddy Ducks or development of chironomid larvae, motivates patch switching (Tome 1988, 1989). Tome (1981) observed that foraging Ruddy Ducks dive repeatedly in the same portion of a wetland until the location is abandoned, after which dive interval increases until another suitable site is found and intensive foraging resumes. Variation in rate of exogenous nutrient acquisition may mean that individual females show variable rates of decline in nutrient reserves during RFG. Nutrient reserves may be critical in ensuring an uninterrupted source of egg nutrients when individual females face shortfalls in exogenous nutrients over a short time interval. Our estimates of rate of decline in nutrient reserves (Table 4) no doubt are confounded by these other factors, but the estimates may nevertheless be thought of as the population average for the rate of nutrient reserve decline in response to egg nutrient demand. Inter-female variability in availability of exogenous nutrients is probably the most important factor confounding the relation between nutrient supply to eggs and decline in nutrient reserves, resulting in a low coefficient of determination for these regressions (Table 4). These considerations probably apply to most birds where a mixed strategy of endogenous and exogenous nutrients are used for eggs, but likely are more pronounced in Ruddy Ducks than in other waterfowl; this is because a female Ruddy Duck rarely leaves the wetland in which its nest is located (Tome 1984), and an important characteristic of habitat quality is the invertebrate prey assemblage associated with that wetland.

Another source of among-female variation in use of reserves for egg production in Ruddy Ducks could be related to their proclivity to lay eggs in nests of conspecifics or of other species (Siegfried 1976a, Joyner 1983). If, for example, in a given year some females are nesters and others are parasites, then these groups could differ in their use of reserves. Some female Ruddy Ducks apparently lay eggs even though unpaired (Gray 1980), and these may be parasites. Female Ruddy Ducks in poor body condition may lay eggs parasitically in nests of other Ruddy Ducks, as has been suggested for other waterfowl (Laughlin 1975, Pienkowski and Evans 1982). If so, they then could use up all their reserves to produce eggs as no reserves would be required for incubation. The preponderance of parasitic egg-laying among yearlings, as has been described in Barrow's and Common Goldeneyes (*Bucephala islandica* and *B. clangula*, Eadie 1989) and Canvasbacks (*Aythya valisneria*, Sorenson 1993), if also true for Ruddy Ducks, may also explain our finding that yearlings become systematically under-represented in our categories of chronologically ranked reproductive states, i.e., from NONRFG to later incubation (Table 1).

We could not evaluate annual variation in nutrient reserve use with our data. The year of our study was about average in wetland conditions at Minnedosa, Manitoba, but exceptional in nesting effort by Ruddy Ducks (see METHODS). Patterns uncovered among Ruddy Ducks breeding in 1988 probably typify those to be found in a variety of years. Annual variation in suitable habitat likely affects the proportion of females that surpass the nutrient reserve threshold (see below), and that subsequently breed. We suggest that this has greater consequences for nesting population size and recruitment of young than do subtle annual changes in rate of nutrient reserve decline for egg production.

PRENESTING STORAGE OF NUTRIENT RESERVES

Our findings suggest that sufficient nutrient reserves are a prerequisite for start of RFG in female Ruddy Ducks. In 1988, there was a one month interval between first arrival (25 April) and first nesting (26 May) and the highest rate of nest initiation occurring in mid-June. In California, Ruddy Ducks stored body fat after arrival on nesting areas (Gray 1980). Tome (1984) reported lower lipid and mineral reserves in "arriving" than in "prelaying" females and interpreted this as storage. He gave no information, however, about timing of collections of birds in each of these categories, potentially confounding conclusions about storage with those about lower nutrient reserves of non-breeders as compared to breeders. We did not sample Ruddy Ducks upon first arrival, so we have incomplete information about amounts of nutrients stored on nesting areas before nesting versus amounts stored during spring migration. Regardless, our data show that, early in the nesting season, breeders were fatter and more muscular than were non-breeders on comparable dates, and that non-breeders stored nutrients after arrival on nesting areas (Fig. 3). Thus, average schedules of nutrient storage were confounded by individual variation, with some individuals attaining adequate reserves for nesting well before others. We suspect that additional variation in prenesting body composition results from differential feeding efficiency of individual females because of experience, age (see below), or access to abundant food. Prenesting nutrient storage may also explain why most Aythyini (diving ducks) show a prolonged interval between arrival and nesting (Hochbaum 1944, Alisauskas et al. 1990, Barzen and Serie 1990, Afton and Ankney 1991), compared to some dabbling ducks (e.g., Mallard and Northern Pintail), which arrive on nesting areas with relatively large nutrient reserves and nest shortly thereafter (Krapu 1974, 1981).

Ruddy Ducks are unusual among North American anatids, because pairing occurs on the breeding grounds, and, apparently, males often provide females with little more than gametes as there is great variation in duration and existence of identifiable pair bonds (Hochbaum 1944, Siegfried 1976b, Gray 1980). Rohwer and Anderson (1988) proposed that evolution of pair formation schedules in waterfowl involved a balance of (a) benefits to females (nutrient acquisition) and to males (mate access), against (b) costs to paired males of mate defense and vigilance (see also Afton and Sayler 1982). Thus, Ruddy Ducks fit this pattern in an extreme way by delaying courtship and pairing until after arrival onto nesting grounds, where some nutrient storage occurs (Gray 1980; Tome 1984, this study). The spatio-temporal unpredictability of prey important for nutrient storage by females, and as a direct source of exogenous nutrient for eggs, may make territorial defense by males uneconomical. Instead, when Ruddy Ducks form identifiable pair bonds, males only defend the female and an area immediately around her (Siegfried 1976a, 1976b).

Tome (1984) hypothesized that nutrient storage in Ruddy Ducks is deferred until after spring migration because high wingloading (Raikow 1973) may hinder efficient migratory flight if nutrients were stored before or during migration. However, Ruddy Ducks shot during fall migration at Long Point ($n > 100$), Ontario, an important staging area, appeared as fat as prelaying ducks collected in Manitoba (Alisauskas and Ankney, pers. observ.). It is unclear to us why excessive wingloading would be a factor in reserve storage during spring, but not fall migration. An alternative hypothesis is that food is more limiting during spring migration. Outside the breeding season, Ruddy Ducks consume animal matter primarily (Euliss et al. 1991, Hoppe et al. 1986), but can consume a variety of seeds and submerged aquatic vegetation (Bellrose 1976 and references therein). Aquatic vegetation is not very abundant in spring due to overwinter mortality of shoots. During winter, many prairie wetlands freeze to the bottom and, during spring thaw, bottoms of wetlands which are open at the surface are frozen, thereby restricting access to submergent macrophytes, root stalks and tubers. Under such conditions, Ruddy Ducks, which are benthic invertebrate specialists during breeding, may face severe food shortages. As benthic invertebrates are the last foods to become available in spring, food inaccessibility on spring staging areas may explain why Ruddy Ducks are among the latest migrants in spring (Hochbaum 1944). Similarly, but due instead to the low quality of an alternate food base, Lesser Scaup (*Aythya affinis*), which show a similar seasonal discrepancy in fatness (A. D. Afton, pers. comm.), may also face chronic food shortages during spring migration preventing proper conditioning for nesting until after arrival on nesting areas (Afton and Ankney 1991).

CONTROL OF REPRODUCTION

By comparing number of visible females ($n = 50$) with number of nests found ($n = 40$) on his study area, Siegfried (1976a) concluded that 20% of Ruddy Ducks did not nest. Based on collections of a few birds, he suggested that food shortages did not limit onset of nesting in Manitoba. Gray (1980) found that nesting activity of female Ruddy Ducks in California occurred about two weeks after numbers of chironomid larvae peaked in nesting areas; she offered this as evidence that availability of exogenous nutrients plays an important role in motivating Ruddy Duck females to nest. Our data indicate that non-breeding is related to size of nutrient reserves, but we suspect that nesting attempts are probably governed by both appropriate levels of nutrient reserves, and food abundance on nesting wetlands relative to nutrient demands for egg formation. Siegfried (1976a) suggested that availability of green vegetation for nesting habitat limited nesting activity of Ruddy Ducks, but we think that nutrient availability, either from nutrient reserves (Table 4) or directly from food (particularly chironomid larvae), is far more important in this regard.

To forgo breeding has greater consequences for lifetime reproductive success than does variation in clutch size, whether it is argued that nutrient reserves are important in controlling such variation (Ankney et al. 1991) or irrelevant to such variation (Arnold and Rohwer 1991). Thus, Arnold and Rohwer's (1991) argument that nutrient reserves are unimportant in control of clutch size is seriously flawed because they ignored nonbreeding (functionally a clutch size of zero). Ecological costs and benefits involved in evolution of nutritionally based thresholds for breeding are unknown, but likely entail low inclusive fitness associated with small clutches, reinforced by predation risk for both clutches and females, a general and important feature of waterfowl nesting ecology (Arnold et al. 1987, Sargeant and Raveling 1992).

Reynolds (1972) first hypothesized that there is a nutrient threshold for reproduction by waterfowl, and his model incorporated covariation in clutch size and laying date. Consequently, nutrient reserve thresholds for initiation of egg laying have been reported for Ring-necked Ducks (*Aythya collaris,* Alisauskas et al. 1990), Gadwalls (*Anas strepera,* Ankney and Alisauskas 1991b) and Ruddy Ducks (this study). As these also were the only studies that have tested the hypothesis, we predict that such thresholds are a general feature of reproduction by temperate and arctic nesting waterfowl. Moreover, we clearly documented a seasonal decline in nutrient reserve thresholds for initiation of breeding. Adaptive reasons for such a decline are less clear, however, but may be related to an interplay between seasonal changes in food abundance and seasonal changes in recruitment rates. We suspect that postfledging survival of young probably is diminished in Ruddy Ducks that nest late, as has been demonstrated in other waterfowl (see Rohwer 1992 for a review), and this should result in selection for early nesting. We believe that Ruddy Ducks have evolved the capacity to nest before exogenous nutrients are abundant if they can succeed in storing sufficient nutrient reserves. Birds able to store enough fat to surpass the early season threshold are the first to nest; birds that store fat at a slower rate after arrival nest later, but, in this case, less cumulative fat will be necessary to initiate breeding because exogenous food is more abundant (see Alisauskas and Ankney 1992). As the nesting season progresses, initiation thresholds, perhaps governed endocrinologically, decline so that a breeding effort becomes more likely even with fewer fat reserves. Our analyses (Fig. 3, Tables 3, 4) suggest that fat reserves decline seasonally, but given that nutrient reserves are stored during the prelaying period, we suspect that birds merely begin to nest after having stored less reserve when nesting late as

TABLE 5. Egg nutrient demand relative to somatic tissue levels in temperate nesting waterfowl. Amount of somatic nutrient was determined as the intercept of regressions of nutrient reserves on clutch nutrients. When those values were unavailable, we used the average present in prelaying females with rapidly developing follicles, unless indicated otherwise in footnotes.

Species	(Egg nutrient/somatic nutrient) × 100		
	Mineral	Lipid	Protein
Ruddy Duck[a]	33.1	9.7	7.0
Lesser Scaup[b]	14.0	10.1	4.2
Gadwall[c]	12.4	5.5	4.6
Shoveler[d]	14.6	7.7	5.9
Ring-necked Duck[e]	17.2	7.8	4.6
Canvasback[f]	—[h]	5.7	4.3
Redhead[g]	—	5.0	4.5
Mallard[i]	16.6	4.0	2.9

[a] This study (Table 6), Alisauskas and Ankney (1994).

[b] Afton and Ankney (1991).

[c] Ankney and Alisauskas (1991b:801); the average ash content of 26.5 g was used as the estimate of somatic mineral in prelayers.

[d] Ankney and Afton (1988).

[e] Alisauskas et al. (1990, unpubl. data).

[f] Barzen and Serie (1990); somatic tissue estimated from intercepts reported for regressions of nutrient reserves vs. mass of largest developing follicle in prelayers.

[g] Alisauskas and Ankney (1992), Noyes and Jarvis (1985).

[h] Not available.

[i] Young (1993); somatic tissue estimated from mean of intercepts reported for regressions of nutrient reserves vs. reproductive nutrients.

opposed to early in the season. Fat reserves were used at the same rates for egg formation regardless of when ducks initiated clutches, although, again, ducks nesting later did so with lower fat reserves than did those nesting earlier. Declining fat reserves with lateness of nesting is in turn related to a seasonal decline in clutch size. Ruddy Ducks may continue to nest late, laying smaller clutches, because some fitness may accrue to them, even though it likely is diminished.

We believe that less protein and mineral reserve is used later for eggs because of seasonal increases in the exogenous availability of these nutrients. For example, emergence of adult chironomids, preceded by maximum instar size of larvae, in Manitoba is greatest in June or July, although there can be marked annual variation in chronology of emergence (Wrubleski and Rosenberg 1990). Some Ruddy Ducks consumed many leeches (Class Hirudinea, Alisauskas and Ankney, unpubl. data), which may also be larger or more abundant as the nesting season progresses. Thus, to begin nesting in May requires greater reliance on endogenous protein than in June, when preferred animal food is likely more abundant. Generally, protein is less limiting than fat because nesting ducks probably select wetlands with abundant protein sources (Alisauskas et al. 1990). We believe that the propensity to nest, timing of nesting and clutch size for individual Ruddy Ducks is an outcome of a complex interaction between ultimate causes (strong selection to nest early) and proximate prerequisites (strong reliance on nutrient reserves). We suspect that there is variation in nesting dates because not all birds are able to surpass nutrient reserve thresholds early in the nesting season due to variable condition at arrival onto nesting areas, and variable rates of nutrient storage after arrival due to variation in wetland quality and individual variation in foraging proficiency. A significant portion of this variation is related to age (see below).

CONTROL OF CLUTCH SIZE

Notwithstanding Arnold and Rohwer's (1991) skepticism, our study shows that nutrient reserves are dually important for egg production, as they influence both nesting propensity and, in the case of mineral reserves, clutch size in Ruddy Ducks. In the case of protein and mineral, lower requisite levels of somatic tissue for clutch formation later in the nesting season was related to greater reliance on exogenous sources of protein and mineral (Figs. 6, 7), so that clutch size *a priori* is not likely related to mineral or protein reserves in late nesters. However, a declining fat threshold was not related to extent to which fat reserves were used to supply clutch fat (Fig. 5). Instead, Ruddy Ducks used fat reserves to supply about half of their clutch nutrients, regardless of nesting date. Also, later-nesting ducks initiated RFG with less fat reserve than did early nesting ducks, such that less fat reserve was available for egg formation. This seasonal decline in available fat reserves is related to, and may explain, the seasonal decline in clutch size of Ruddy Ducks.

Number of developing follicles in females nearing end of laying was correlated with fat reserves in Shovelers (Ankney and Afton 1988), and with protein reserves in Gadwalls (Ankney and Alisauskas 1991b). In Ruddy Ducks, however, number of developing follicles was related to somatic mineral levels, which suggests a major difference in nutrient constraints on Ruddy Ducks compared to these other species. Although feeding ecology (including diet during laying) of all these species is different, demand for minerals during eggshell production by Ruddy Ducks is extraordinary: mass of a single eggshell is a much greater percentage of somatic minerals in prelaying Ruddy Ducks than it is in other species for which data are available (Table 5). Consumption of gastropods, a rich source of minerals, increased from laying to early incubation in female Ruddy Ducks (Alisauskas and Ankney, unpubl. data), presumably to replenish depleted cortical bone (Taylor and Moore 1954).

AGE-RELATED PATTERNS

Older waterfowl generally nest earlier, have higher average clutch sizes and greater breeding propensity than do younger individuals (see Afton 1984, Rohwer 1992:521 and references therein). Age-related variation in nutrient reserves may explain at least some age-related patterns in reproductive rates (Krapu and Doty 1979, Alisauskas and Ankney 1987), but in Ruddy Ducks, it had its greatest effect on propensity to breed. Adults showed greater likelihood of initiating breeding than did yearlings and this was correlated with greater levels of fat and protein reserves of adults. Of females that initiated a laying cycle, no differences were apparent in reserve use between ages. In Gadwalls and Canvasbacks, yearlings began laying cycles with less fat than did adults, and relied less on lipid reserves for egg production than did adults (Ankney and Alisauskas 1991b, Barzen and Serie 1990). In Ruddy Ducks, those yearlings (a minority of them) that surpassed nutrient reserve thresholds for initiation of breeding were indistinguishable from breeding adults in their patterns of nutrient reserve use for egg formation. Because some yearlings breed, and because their breeding propensity is related to their ability to acquire sufficient nutrient reserves, which, in turn, is related to adeptness at foraging, it is likely that breeding constraint rather than restraint is operating as suggested for waterfowl by Rohwer (1992).

CONCLUSIONS

We believe (Alisauskas and Ankney 1992) that three factors were responsible for the evolution of high rates of nutrient secretion by ducks relative to other species. First, it is a necessity for their large nutrient-rich eggs (Lack 1967, 1968). Second, we agree with Arnold et al. (1987) that open-nesting waterfowl have undergone strong selection to reduce the number of days that eggs and females are exposed to predators. Finally, we also think that because of their adaptations for exploiting aquatic invertebrates, most species are capable of avoiding protein shortage by occupying wetlands that are highly productive of such animals (Alisauskas et al. 1990). However, because invertebrate protein is spatially and temporally ephemeral, there is a premium on its rapid exploitation (Alisauskas and Ankney 1992). Most temperate-nesting ducks obtain exogenous protein at a rate enabling production of one egg/day, and, other than Gadwalls (Ankney and Alisauskas 1991b) and Ruddy Ducks (this study), they do this without using protein reserves (see Ankney and Alisauskas 1991a, Alisauskas and Ankney 1992 for reviews). (Although many large-bodied waterfowl, such as arctic-nesting geese, may rely extensively on nutrient reserves for clutch formation [e.g., Ankney and MacInnes 1978], there appear to be rate-limiting effects such that egg-laying intervals are >1 day [Alisauskas and Ankney 1992]). Some of this ability is related to differences between diet during the breeding season and other times of the annual cycle (Ankney and Alisauskas 1991a). Although it is physiologically possible to capture and convert animal protein from wetlands directly into egg proteins, it may be ecologically impossible to convert either carbohydrate or protein into egg lipid at a rate sufficient to meet nutrient demands of one egg/day (Alisauskas et al. 1990). Thus, we think that the tactic to store and use body fat is a trait that has coevolved with the evolution of rapid reproductive rates by temperate-nesting ducks in highly productive habitats. Prenesting storage of nutrient reserves also is probably an important factor that can advance nesting seasons before exogenous nutrients reach an abundance that is sufficient to allow reliance on them for forming eggs.

Although Ruddy Ducks use the same landscapes as other ducks nesting in the prairie pothole region of the northern plains of North America, they are extraordinary in their extreme nutrient demand for egg production. The pattern of nutrient reserve use for egg production by Ruddy Ducks fits those of waterfowl in general as use of lipid reserves during egg production is virtually ubiquitous (Ankney and Alisauskas 1991a). However, Ruddy Ducks also showed significant use of both somatic protein (this study) and mineral (Tome 1984, this study) for producing eggs. We believe that predation pressure and ephemeral food sources have been responsible for evolution of rapid nutrient secretion in Ruddy Ducks, as argued for other temperate ducks. Storage and use of fat, protein and mineral reserves, in addition to adaptations for efficient exploitation of benthic invertebrates from highly productive wetlands, enable Ruddy Ducks to produce exceptionally large eggs at a rapid rate. However, proximate limitations on attempted breeding and clutch size operate in many cases because of individual variation in ability to store sufficient nutrient reserves, and to find and exploit high quality patches of aquatic invertebrates.

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