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NUTRIENT-RESERVE DYNAMICS OF BREEDING LESSER SCAUP: A TEST OF COMPETING HYPOTHESES[1]

ALAN D. AFTON[2]
Delta Waterfowl Research Station, R.R. #1, Portage la Prairie, Manitoba R1N 3A1, Canada; and Department of Biology and Institute for Ecological Studies University of North Dakota, Grand Forks, ND 58202

C. DAVISON ANKNEY
Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7, Canada

Abstract. We analyzed nutrient reserves (lipid, protein, mineral) and organs of Lesser Scaup (*Aythya affinis*) breeding in southwestern Manitoba. Our analysis provided weak support for the hypothesis that paired males are physically superior to those pairing later or not at all. Protein reserves of paired males were larger than those of unpaired males, whereas fat and mineral reserves were similar in size between pair-status groups. Except for a marked decline in lipid reserves, body components and organs of paired males changed little while on breeding areas before laying by their mates. Nutrient reserves of males also did not change relative to the nutrient commitment to reproduction by their mates. Females accumulated protein and mineral reserves and at least maintained lipid reserves while on breeding areas before laying. Lipid reserves of females declined, on average, 0.5 g for every 1 g of lipid deposited in eggs. Mineral reserves declined, on average, 0.1 g for every 1 g of egg shell produced. Declines in nutrient reserves of incubating females could account for 12% of their energy requirements during that period. Lipid-reserve dynamics of females were consistent with predictions of the lipid-limitation hypothesis, but contradicted those of the protein-limitation and migrational-uncertainty hypotheses. Food availability on breeding areas may limit lipid storage by females, and serve as an important proximate factor affecting clutch size of Lesser Scaup.

Key words: Lesser Scaup; nutrient reserves; organs; male pair status; clutch-size limitation; incubation; food availability.

INTRODUCTION

Utilization of exogenous and endogenous nutrients by breeding waterfowl presently is a topic of considerable research and scientific debate (Alisauskas and Ankney, in press; Rohwer, in press). Three hypotheses have been proposed to explain nutrient-reserve dynamics during egg formation by prairie-nesting ducks. The "protein-limitation hypothesis" (Drobney 1980, Krapu 1981, Drobney and Fredrickson 1985) suggests that female ducks utilize lipid reserves while foraging inefficiently on aquatic invertebrates to meet protein requirements for egg production. In contrast, the "lipid-limitation hypothesis" (Ankney and Afton 1988; Alisauskas et al., in press) states that lipids, not protein, directly limit clutch size, in part because female ducks forage in highly productive wetlands where protein (e.g., invertebrates) is easier to obtain than are lipids during spring. The "migrational-uncertainty hypothesis" (Rohwer 1986, in press) suggests that waterfowl store fat to assure that they have energy for migration and as a hedge against unfavorable weather upon arrival on breeding areas. Because migratory waterfowl generally breed shortly after arrival, this hypothesis argues that females simply dump unneeded lipid stores into a clutch of eggs (Rohwer 1986, in press)

Lesser Scaup (*Aythya affinis,* hereafter called scaup) are ideal subjects for examining predictions of these competing hypotheses. Diets of scaup are comprised primarily of aquatic invertebrates throughout the annual cycle (Afton 1983, 1984; Afton et al., in press); thus, we assume that scaup forage efficiently on such prey. Accordingly, the protein-limitation hypothesis predicts that female scaup require relatively small lipid reserves during egg formation (cf. Ankney and Afton 1988), whereas females should utilize considerable endogenous lipids under the lipid-lim-

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[2] Present address: U.S. Fish and Wildlife Service, Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana State University, Baton Rouge, LA 70803.

itation hypothesis. Unlike many other ducks, female scaup spend lengthy periods (mean = 35.5 days, Range = 21–56) on breeding areas before laying eggs (Afton 1984). Consequently, the migrational-uncertainty hypothesis predicts that lipid reserves of female scaup should decline before egg laying, whereas females should maintain or further accumulate lipids under the other hypotheses.

In this paper, we analyze nutrient reserves (lipid, protein, mineral) and organs of scaup breeding in southwestern Manitoba, and discuss the results in light of predictions from these competing hypotheses. We also analyze nutrient reserves and organs of males in relation to their pair status to test the hypothesis (Wishart 1983) that paired individuals are physically superior to those pairing later or not at all.

STUDY AREA AND METHODS

Data presented are from 40 male and 46 female scaup collected from April to July, 1977–1981 near Erickson, Manitoba (50°30'N, 99°55'W). Detailed descriptions of the area are provided in Rogers (1964), Hammell (1973), and Sunde and Barica (1975).

BREEDING STATUS

We shot foraging pairs and unpaired males from spring arrival through the laying period. Male pair status was determined by behavioral criteria before collection (Afton 1985). Incubating females were flushed from nests and shot, and stage of incubation (days) was determined from known egg dates or by aging embryos (Caldwell and Snart 1974). Collections were initiated each year only after marked residents arrived and unmarked migrants departed from an intensive behavioral study area (Afton 1984, 1985) to ensure that specimens represented birds breeding in the area.

Scaup were weighed (±1 g) immediately after collection (=fresh body weight), and esophageal-proventricular contents were removed for another study. Specimens were then labeled, placed in double plastic bags, and frozen until subsequent processing.

For analysis, females were assigned to various categories of the reproductive cycle: 1) pre-Rapid Follicle Growth (pre-RFG; dry weight of largest ovarian follicle < 0.2 g), 2) Rapid Follicle Growth (RFG; largest follicle ≥ 0.2 g), 3) Laying (in RFG with 1 or more postovulated follicles), and 4) Incubation. Paired males were classified according to reproductive categories of their mates. Our method for estimating the initiation of RFG was developed as follows: 1) laying females (n = 8) with a complete set of developing follicles (max = 6) were examined; and 2) mean dry weight (see below) of the second smallest, developing follicle was calculated and used as the criterion (mean = 0.20 g, SE = 0.02).

BODY COMPOSITION AND ORGAN ANALYSES

Specimens were thawed and six measurements taken: 1) *keel length* (±0.1 mm), 2) *total length* (±1 mm) from tip of longest retrix to tip of bill with bird stretched on its back, 3) *bill length* (±1 mm) from rictus to nail edge, 4) *culmen* (±0.1 mm), 5) *wing length* (±1 mm) as described by Carney (1964), and 6) *right tarsus* (±0.1 mm). The following components were then dissected free of visible fat: breast and leg muscles from the right side (Ankney and MacInnes 1978), heart, gizzard, liver, and intestine (combined small intestine, caeca, and colon). Reproductive organs also were removed and saved for subsequent analysis (see below). Intestine length (from gizzard to cloaca) was measured (±1 mm) and wet weights (±0.1 g) were taken on all parts. Contents of gizzard and intestine were removed, and these organs were reweighed (±0.1 g). Contents of esophagus, proventriculus, gizzard, and intestine were summed and reported as ingesta. Heart, gizzard, and intestine were dried to constant weight at 90°C (Kerr et al. 1982), and subsequently returned to the carcass.

The carcass (i.e., excluding reproductive organs, liver, and right breast and leg muscles) was then ground three times using three different-sized plates (10, 5 and 3 mm) in a Hobart meat grinder. A 100-g sample of this carcass homogenate, and the entire liver, and breast and leg muscles were dried separately to constant weight at 90°C. The dried carcass homogenate, liver, and breast and leg muscles were then homogenized separately again with the Hobart grinder (3 mm plate).

Proximate analysis of carcass homogenate, liver, and breast and leg muscles was done as detailed by Alisauskas and Ankney (1985). For each bird this involved: 1) removing lipids from a subsample (ca. 10 g) of each constituent using petroleum ether as a solvent (Dobush et al. 1985) in a modified Soxhlet apparatus, 2) multiplying the dry weight of each constituent by the proportion of lipid that it contained (derived from Step 1) to determine its total lipid weight, and

3) subtracting total lipid weight from the dry weight of each constituent to determine its lean dry weight (LDW). Lean dry samples of carcass homogenate (6–9 g) were ashed in a muffle furnace at 550°C for 6 h. The proportion of ash in each sample was used to calculate the total ash (ASH) in the carcass of each bird. ASH was subtracted from LDW of each carcass to obtain ash-free lean dry weight (AFLDW), an index of protein (Mainguy and Thomas 1985, p. 1767). Thus, for each bird:

$$\text{PROTEIN} = \text{AFLDW}_{\text{carcass}} + \text{LDW}_{\text{leg}} + \text{LDW}_{\text{breast}} + \text{LDW}_{\text{liver}}$$

and

$$\text{FAT} = \text{fat}_{\text{carcass}} + \text{fat}_{\text{leg}} + \text{fat}_{\text{breast}} + \text{fat}_{\text{liver}}.$$

Ash contents of the liver and breast and leg muscles were assumed to be negligible (Robbins 1983, p. 211). ASH, PROTEIN, and FAT are herein referred to as nutrient reserves, which are defined as the measure of the fraction (fat, protein or mineral) of the whole bird which may respond to changes in energy/nutrient balance (Alisauskas and Ankney 1985, p. 134).

REPRODUCTIVE TISSUE ANALYSIS

Right and left testes were dried separately to constant weight at 90°C and discarded. If present, eggs were removed from oviducts, and oviducts were dried to constant weight at 90°C and discarded. Number of postovulated follicles (NPOF) on each ovary were counted. Each rapidly developing follicle was then excised (max = 6), and individual follicles and remainder of the ovary were dried separately to constant weight at 90°C. Lipids were removed from each constituent as described for the carcass. The residue (LDW) of each constituent was used to index protein.

Lipid content and LDW of a few rapidly developing follicles could not be determined by extraction techniques because of shot damage. Thus, we calculated relationships between mass of an intact follicle and the next smallest intact follicle in the hierarchy (Walford 1946). Lipid ($\text{Fat}_{\text{follicle}}$) and protein contents ($\text{LDW}_{\text{follicle}}$) of damaged follicles were then estimated from the following equations:

$$\text{Fat}_{\text{follicle}} = 0.586 + 1.60(\text{Fat}_{\text{follicle-1}})$$

($n = 28$, $r^2 = 0.95$, $P < 0.0001$), and

$$\text{LDW}_{\text{follicle}} = 0.276 + 1.62(\text{LDW}_{\text{follicle-1}})$$

($n = 28$, $r^2 = 0.96$, $P < 0.0001$), where $\text{Fat}_{\text{follicle-1}}$ and $\text{LDW}_{\text{follicle-1}}$ are lipid and protein contents, respectively, of the next smallest developing follicle on the same ovary.

In estimating nutrient commitment to egg production, we used composition values from a sample of 13 scaup eggs from 13 nests analyzed by Frank Rohwer (pers. comm.). The average egg contained 6.82 g of lipid and 6.91 g of protein. Thus, total commitment of lipids to reproduction (R-FAT) for each female was estimated as:

$$\text{R-FAT} = \sum_{i=1}^{n} \text{Fat}_{\text{follicle}} + \text{Fat}_{\text{ovary}} + 6.82(\text{NPOF})$$

and total commitment of protein to reproduction (R-PROTEIN) was estimated as:

$$\text{R-PROTEIN} = \sum_{i=1}^{n} \text{LDW}_{\text{follicle}} + \text{LDW}_{\text{ovary}} + \text{DW}_{\text{oviduct}} + 6.91(\text{NPOF})$$

where n = number of rapidly developing follicles, $\text{Fat}_{\text{ovary}}$ = lipid content of remainder of ovary, $\text{LDW}_{\text{ovary}}$ = lean dry weight of remainder of ovary, and $\text{DW}_{\text{oviduct}}$ = dry weight of oviduct. Total commitment of mineral reserves to reproduction (R-ASH) was estimated by multiplying NPOF by 4.08, the mean dry weight of shell (Frank Rohwer, pers. comm.).

BODY SIZE

We performed principal components analysis of the correlation matrix for the six measurements taken on each specimen (PROC PRINCOMP, SAS Institute Inc. 1987). The first principal component (PC1) for the six variables described positive correlation in all measures with loadings ranging from 0.30 to 0.51. The corresponding eigenvalue was 2.40, and PC1 accounted for 40.0% of the total original variance. We interpreted this covariation as variation in size, and used PC1 scores for each bird as a measure of its body size.

STATISTICAL ANALYSIS

Samples within each year of the study were inadequate (i.e., missing cells) for a factorial analysis of the influence of year and reproductive stage on nutrient reserves. One-way analyses of variance indicated that nutrient reserves within each reproduction stage were similar (all P values > 0.08) among years for males and females. Furthermore, lack-of-fit analyses (Freund et al. 1986, p. 117) indicated that year effects did not con-

tribute significantly (all P values > 0.20) to a single factor (i.e., reproductive stage) model of nutrient reserves for males or females. Accordingly, we pooled data over years for subsequent analyses.

Comparisons of mean nutrient reserves between discrete reproductive categories underestimate changes in the size of nutrient reserves (Alisauskas and Ankney, in press). However, comparisons between pre-RFG and RFG stages for scaup are useful in detecting relative changes in nutrient reserves after arrival on breeding areas because of the lengthy interval between arrival and laying (Afton 1984). We used t-tests to compare nutrient reserves and organs between pre-RFG and RFG males and females, and between paired and unpaired males. Regression analysis was used to detect changes in nutrient reserves during egg production and incubation (Alisauskas and Ankney, in press). When warranted, dependent variables were scaled to body size as described by Ankney and Afton (1988; note that the last term of their adjustment equation should have been *mean* of Y observations).

RESULTS

BODY COMPOSITION AND ORGANS BY MALE PAIR STATUS

Fresh body weights of paired males were larger than those of unpaired males, apparently because of differences in protein reserves and ingesta (Table 1). Differences in protein reserves partially were due to LDWs of breast and leg, but not of liver. Other nutrient reserves and organs were similar in size between pair-status groups.

BODY COMPOSITION AND ORGANS ON BREEDING AREAS BEFORE LAYING

Fresh body weight of females increased between pre-RFG and RFG stages, apparently because of increases in reproductive tissue and in mineral and protein reserves (Table 1). Variation in protein reserves of females partially was due to changes in LDW of leg, but not of breast or liver. Organs of females were similar in size between reproductive stages. Except for a marked decline in lipid reserves, body components and organs of paired males also were similar in size between reproductive stages (Table 1).

NUTRIENT-RESERVE DYNAMICS DURING EGG FORMATION

Lipid and mineral reserves of females were negatively related to amounts of these nutrients that they had deposited in ova (Fig. 1). For every gram of R-FAT and R-ASH produced, FAT and ASH declined 0.50 g and 0.13 g, respectively (Table 2). RFG females showed considerable variation in FAT (Fig. 1), and it is possible that some of the "early" hens had not yet entered an uninterrupted laying cycle (see Alisauskas and Ankney, in press). Restricting the analysis to females that had laid eggs suggested a greater reliance on lipid reserves for egg production because the slope estimate nearly doubled (FAT = $89.0 - 0.92 \cdot$R-FAT, $n = 13$, $r^2 = 0.45$, $P = 0.005$). Protein reserves of females did not change relative to nutrient commitment to reproduction in the overall sample (Table 2). However, females that had laid at least one egg showed an increase in PROTEIN with increased R-PROTEIN (PROTEIN = $151.5 + 0.25 \cdot$R-PROTEIN, $n = 13$, $r^2 = 0.27$, $P = 0.049$). Nutrient reserves of males did not change relative to the nutrient commitment to reproduction by their mates (Table 2).

NUTRIENT-RESERVE DYNAMICS DURING INCUBATION

Incubating females, on average, lost 5.33 g/day (Table 3), i.e., about 139 g or 20% of initial body weight during the 26-day incubation period (Afton 1983). Fat declined 0.88 g/day during incubation, i.e., about 23 g, which was 17% of total loss in body weight. Protein declined 0.81 g/day, whereas mineral reserves did not change during incubation. Given that muscle is 75% water and 25% protein (Ankney, unpubl. data), the decline in protein (21 g) would result in a loss of 84 g of body weight (60% of total loss).

DISCUSSION

MALE PAIR STATUS

Wishart (1983) hypothesized that paired birds were physically superior to those pairing later or not at all, and reported that data from captive and wild American Wigeons (*Anas americana*) were consistent with this hypothesis. Male characteristics that were important in acquiring a mate included age, size, plumage, and body condition (Wishart 1983; see also McKinney, in press). Our analysis of male scaup provided weak support for this hypothesis. Protein reserves of paired males were larger than those of unpaired males. Although fat reserves were not statistically different between groups, estimated means varied in the predicted direction. However, body size (indexed by ASH or PC1) was similar between

TABLE 1. Body composition and organs (mean ± SE) of Lesser Scaup breeding in southwestern Manitoba.

Variable[a]	Females			Males					
	Pre-RFG (n = 15)	P[b]	RFG (n = 6)	Pre-RFG (n = 15)	P[b]	RFG (n = 4)	Paired (n = 30)	P[b]	Unpaired (n = 10)
Body composition									
Body weight (fresh)	730.0 ± 14.0	*	787.3 ± 14.4	752.4 ± 21.6	ns	735.0 ± 11.5	735.1 ± 11.7	*	680.1 ± 25.4
Body weight (corrected)[c]	700.7 ± 13.8	ns	721.8 ± 13.0	732.8 ± 21.0	ns	709.9 ± 11.3	711.8 ± 11.6	ns	666.8 ± 25.0
Ingesta weight	25.4 ± 2.0	ns	29.5 ± 4.0	16.8 ± 1.7	ns	20.9 ± 3.6	19.4 ± 1.5	*	10.2 ± 1.3
FAT	59.3 ± 7.9	ns	57.8 ± 11.5	82.2 ± 12.9	*	25.3 ± 7.1	55.0 ± 8.3	ns	46.0 ± 11.0
ASH	25.9 ± 1.0	*	30.2 ± 1.4	25.1 ± 1.2	ns	27.3 ± 2.2	26.8 ± 0.9	ns	28.6 ± 1.4
PROTEIN	156.0 ± 1.5	*	167.1 ± 5.0	165.9 ± 2.7	ns	174.0 ± 4.9	166.4 ± 2.0	***	146.7 ± 5.0
Breast LDW	15.7 ± 0.3	ns	16.6 ± 0.3	16.7 ± 0.4	ns	16.5 ± 0.4	16.4 ± 0.2	**	14.6 ± 0.7
Leg LDW	5.8 ± 0.1	*	6.4 ± 0.3	6.2 ± 0.1	ns	6.5 ± 0.1	6.3 ± 0.1	**	5.6 ± 0.2
Liver LDW	5.3 ± 0.3	ns	5.2 ± 0.4	4.7 ± 0.4	ns	4.4 ± 0.3	4.7 ± 0.2	ns	4.2 ± 0.2
Organs									
Heart weight[d]	1.8 ± 0.1	ns	1.7 ± 0.1	1.8 ± 0.1	ns	1.8 ± 0.2	1.8 ± 0.1	ns	1.7 ± 0.1
Liver weight[d]	5.7 ± 0.3	ns	5.7 ± 0.5	5.1 ± 0.4	ns	4.7 ± 0.4	5.0 ± 0.2	ns	4.5 ± 0.2
Gizzard weight[d]	6.0 ± 0.3	ns	6.4 ± 0.5	5.7 ± 0.2	ns	6.0 ± 0.4	5.7 ± 0.2	ns	5.8 ± 0.4
Intestine weight[d]	5.4 ± 0.3	ns	6.0 ± 0.5	5.1 ± 0.3	ns	4.0 ± 0.5	4.7 ± 0.2	ns	4.9 ± 0.6
Intestine length	1,898.2 ± 30.2	ns	1,857.3 ± 43.2	1,758.3 ± 41.3	ns	1,833.8 ± 88.7	1,762.2 ± 29.4	ns	1,712.0 ± 52.7

[a] Lengths in mm and weights in g.
[b] Probability levels from t-tests between adjacent columns; * = $P < 0.05$, ** $P < 0.01$, *** = $P < 0.001$, ns = $P > 0.05$.
[c] Corrected body weight is weight of bird minus ingesta and reproductive tissue.
[d] Dried to constant weight.

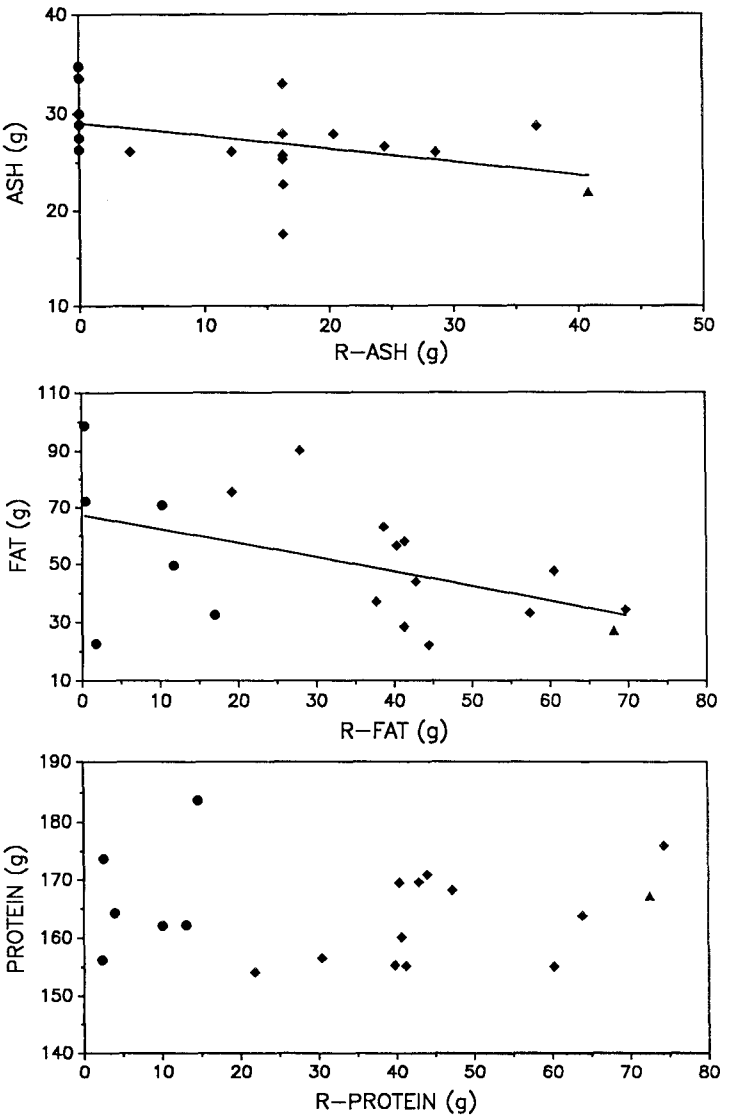

FIGURE 1. Relation between ASH, FAT, and PROTEIN (scaled to body size—see Methods) reserves of female Lesser Scaup (Y-axes) and their corresponding commitment of those nutrients to egg production (X-axes). Equations describing these relationships are in Table 2. Analyses included 6 RFG (circles) and 12 laying females (diamonds), and 1 incubating female (triangle) collected the day following completion of her clutch.

pair-status groups. Unfortunately, we have no data on age or plumage variation in our sample.

NUTRIENT-RESERVE DYNAMICS AND HYPOTHESIS TESTS

Lipid reserves of paired males declined markedly while on breeding areas before laying by their mates. This decline in reserves was correlated with changes in time-activity budgets of paired males. During this period, males decreased feeding time and increased time spent alert and in mate-guarding (Afton 1985, unpubl. data).

Female scaup accumulated protein and mineral reserves, and at least maintained lipid reserves while on breeding areas before laying. Accordingly, we reject the migrational-uncertainty

TABLE 2. Equations (from least squares regression) relating size of female nutrient reserves to her nutrient commitment to reproduction, and size of male nutrient reserves to nutrient commitment to reproduction by his mate.[a]

Y	X	Intercept	Slope	r^2	P^b
Females (n = 19)					
ASH	R-ASH	29.06 (1.32)[c]	−0.13 (0.08)	0.18	0.049
FAT	R-FAT	67.3 (8.6)	−0.50 (0.22)	0.24	0.016
PROTEIN[d]	R-PROTEIN	163.6 (3.6)	+0.02 (0.09)	0	0.94
Males (n = 14)					
ASH	R-ASH	28.43 (2.52)	+0.01 (0.14)	0	0.99
FAT	R-FAT	26.4 (8.2)	+0.05 (0.20)	0	0.95
PROTEIN	R-PROTEIN	169.4 (6.7)	−0.05 (0.16)	0.01	0.89

[a] Female analyses include 6 RFG and 12 laying females, and 1 incubating female collected the day following completion of her clutch; male analyses include males paired to the above females.
[b] Probability that $r = 0$.
[c] (1 SE).
[d] Scaled to body size—see Methods.

hypothesis (Rohwer 1986, in press) in explaining lipid-reserve use during egg formation. Mineral reserves of females declined slightly during egg-laying, accounting for the shell of one egg in an average 10 egg clutch (Afton 1984). Despite the ability of female scaup to obtain more protein than needed for egg formation, they utilized considerable amounts of lipid reserves, i.e., their utilization must have involved factors other than difficulty in obtaining aquatic invertebrates. Consequently, we also reject the protein-limitation hypothesis, and conclude that nutrient-reserve dynamics of female scaup during egg formation are consistent with predictions of the lipid-limitation hypothesis.

Although comparisons of pre-RFG and RFG females provided no evidence that lipid reserves were accumulated after arrival on breeding areas, we suspect that some storage may have occurred. Several RFG females had committed >10 g of lipids to reproductive tissue (see Fig. 1); thus, using a mean value for this category certainly underestimated total lipid reserves accumulated prior to laying (see also Alisauskas and Ankney, in press).

INCUBATION ENERGETICS

Afton and Paulus (in press) estimated that the total energy required for incubation by female scaup was 10,065 kJ. Catabolism of lipids and protein yields 37.7 kJ/g and 18.0 kJ/g (Ricklefs 1974), respectively. Thus endogenous reserves provide, on average, 12% of the total energy required during incubation. Our estimate is lower than that predicted (19%) from female body weight at the start of incubation (Afton and Paulus, in press), i.e., use of endogenous reserves by incubating female scaup is relatively lower than that of other waterfowl of similar size.

Reliance on environmental foods by female scaup, to support their metabolism during incubation, probably is facilitated by their late-nesting chronology (Afton 1984) and increasing food availability during the breeding season (see below). This reliance on food during incubation may be advantageous in allowing females to: 1)

TABLE 3. Linear regressions relating fresh body weight and nutrient reserves (Y) to day of incubation (X) for female Lesser Scaup (n = 13) in southwestern Manitoba.

Variable	Intercept	Slope	r^2	P^a
Body weight (fresh)	697.9 (16.4)[b]	−5.33 (1.44)	0.55	0.001
ASH	21.99 (2.36)	+0.10 (0.21)	0.02	0.80
FAT	31.4 (3.5)	−0.88 (0.30)	0.43	0.0006
PROTEIN[c]	162.3 (3.77)	−0.81 (0.33)	0.35	0.017

[a] Probability that b = 0.
[b] (1 SE).
[c] Scaled to body size—see Methods.

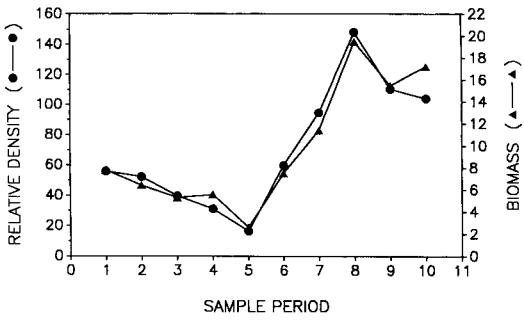

FIGURE 2. Mean relative density (individuals/net sweep) and biomass (g dry weight/net sweep) of *Gammarus* for nine ponds near Erickson, Manitoba (summarized from Austin 1983: Table 5). Sample periods represent bimonthly sampling from 30 May (period 1) through 8 October 1982 (period 10).

increase clutch size by allocating a greater proportion of their endogenous reserves to eggs, and/or 2) improve body condition for migration more quickly upon completion of brood-rearing and molt.

CONCLUSIONS

Our results strongly suggest that lipid reserves, not protein availability, limit clutch size of scaup. Moreover, evidence is accumulating that temperate-nesting ducks generally are lipid limited and not protein limited during egg production (see review by Ankney and Alisauskas, in press). Our data, plus those for Canvasbacks (*Aythya valisineria*) (Barzen and Serie 1990) and Gadwalls (*Anas strepera*) (Ankney and Alisauskas, unpubl. ms.), contradict predictions of the migrational-uncertainty hypothesis and indicate, at the least, that this hypothesis lacks generality.

If lipid reserves limit clutch size of scaup, then it is important to ask why, on average, these birds do not begin laying with larger reserves. Lipid reserves of female scaup on our study area in fall averaged 188.1 g (Austin and Fredrickson 1987), or about three times larger than that of females just before laying (Table 1). Thus, breeding females could easily carry larger lipid stores.

Lipid content of *Gammarus lacustris,* the predominant food on the study area (Afton 1983, 1984; Austin 1983), was similar during the period that scaup lay eggs (June, 0.9% wet weight) and fall (September–October, 0.9%) (Austin 1983). However, relative density and biomass of *Gammarus* in area ponds were much higher in fall than during the scaup breeding season (Fig. 2; see Austin 1983). Relative density of *Gammarus* averaged about 50 individuals/net sweep during the breeding season and increased roughly three-fold by early fall. Biomass averaged about 6 g/net sweep during the breeding season and also increased by a factor of three in fall.

We conclude that food availability during the breeding season may limit lipid storage by females, and serve as an important proximate factor affecting clutch size of scaup (cf. Ankney and Afton 1988). We also concur with Alisauskas et al. (in press) that lipid storage by temperate-nesting ducks has evolved so that clutch lipids can be supplied at a high daily rate, and that high densities of aquatic invertebrates in breeding habitats of these ducks allow a concomitant high rate of clutch-protein production. Our data showing that female scaup stored protein during egg-laying, when protein demand is highest, supports this conclusion.

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