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NUTRIENT-RESERVE DYNAMICS AND CONTROL OF CLUTCH SIZE IN NORTHERN PINTAILS BREEDING IN ALASKA

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ABSTRACT.—We collected breeding Northern Pintails (*Anas acuta*) in subarctic Alaska during 1987 and 1988 to assess nutrient-reserve dynamics. Greatest body mass of both sexes occurred during the rapid-follicle-growth (RFG) period of females. Males lost lipid, but not protein reserves, between RFG and laying periods. Females lost an average of 94 g of lipid from RFG to early incubation. An average clutch contained less than half the amount of carcass lipid lost between RFG and early incubation; thus, endogenous lipid was used to meet both reproductive and maintenance energy costs. Females lost protein during laying; we estimate endogenous protein provided 21 to 62% of the protein requirement for egg production. Carcass protein reserves were negatively related to the proportion of clutch laid ($P = 0.01$), whereas lipid reserves were not, suggesting that protein limited clutch size. These patterns differ from those for most temperate-breeding ducks, but we are uncertain whether this results from geographic and/or phylogenetic variation. *Received 16 December 1991, accepted 15 November 1992.*

LARGE-BODIED arctic-nesting geese and Common Eiders (*Somateria mollissima*) are thought to be capable of carrying sufficient protein and lipid reserves to enable them to produce and incubate a clutch of eggs (Korschgen 1977, Ankney and MacInnes 1978, Parker and Holm 1990, Alisauskas and Ankney 1992). Small-bodied arctic-nesting geese utilize both stored reserves and exogenous nutrients (Raveling 1979, Ankney 1984). The small body size of ducks reduces the potential size of nutrient reserves relative to maintenance and production requirements, and may preclude them from relying predominantly on stored reserves during egg production. Consequently, when compared to geese, many female ducks studied to date undergo little or no reduction in the size of their protein stores while producing a clutch (Krapu 1981, Reinecke et al. 1982, Tome 1984, Hohman 1986, Ankney and Afton 1988) and rely primarily on exogenous protein for egg production (Krapu 1974, 1981, Drobney 1982, Tome 1984, Hohman 1985, Ankney and Afton 1988). However, female Gadwalls (*Anas strepera*) and Canvasbacks (*Aythya valisineria*) increase invertebrate consumption during the breeding season (Noyes and Jarvis 1985, Serie and Swanson 1976, Ankney and Alisauskas 1991), and also use endogenous protein reserves during egg production (Barzen and Serie 1990, Ankney and Alisauskas 1991).

Drobney (1980) and Krapu (1981) proposed that availability of dietary protein limited egg production in prairie-nesting ducks based on the shift to invertebrate foods during RFG and laying periods. They proposed that Wood Ducks (*Aix sponsa*) and Mallards (*Anas platyrhynchos*) used previously stored lipids to help meet their energy requirements, thus freeing them to concentrate foraging on invertebrates. In this respect, their hypothesis is similar to the one first proposed by Jones and Ward (1976) for Red-Billed Queleas (*Quelea quelea*). Ankney and Afton (1988) showed that Northern Shovelers (*Anas clypeata*) relied heavily on endogenous lipid during egg laying and proposed that lipid, not protein, regulated clutch size in this and possibly other species of ducks. A third hypothesis is that energy, not lipid, per se, limits clutch size in ducks. All data on nutrient-reserve use by ducks (other than Common Eiders; Parker and Holm 1990), however, are from temperate latitudes; little is known about the reproductive physiology of ducks nesting in the Arctic or subarctic.

Nutrient dynamics may differ for ducks nesting at high latitudes compared to those nesting at temperate latitudes. Northern Pintails (*Anas acuta*) generally nest at higher average latitudes

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(Bellrose 1980) than most species of ducks for which nutrient dynamics have been studied. The majority of Northern Pintails nesting in subarctic Alaska winter in California and Mexico (Bellrose 1980). Thus, Alaskan birds may migrate farther than temperate-nesting congeners and may arrive on breeding areas with smaller lipid reserves. Arctic wetlands (Brown et al. 1980, Hobbie 1980) are less productive than those at lower latitudes. Although data are lacking for subarctic wetlands, lower productivity in these wetlands might reduce the ability of subarctic breeders to meet requirements for maintenance and breeding, relative to breeders in temperate environments. Northern Pintails nest early (Sowls 1955, Hooper 1952, Rowinski 1958), which combined with their relatively high latitude breeding distribution may select for a greater reliance on endogenous reserves for egg production (Alisauskas and Ankney 1992). Our objective was to study seasonal lipid and protein dynamics in Northern Pintails and to assess the importance of stored reserves for breeding in subarctic wetlands.

Methods

Study area.—We collected male and female Northern Pintails from Minto Flats, Alaska (64°50'N, 148°50'W), which is a large wetland complex (approximately 725 km^2) composed of numerous shallow lakes and ponds located about 60 km west of Fairbanks. The average density of Northern Pintails on Minto Flats during the breeding season (16 birds/km^2) is comparable to their highest densities elsewhere in North America (B. Conant and J. I. Hodges unpubl. report). Elevation varies less than 15 meters (Rowinski 1958), and Minto Flats is frequently flooded by high water during spring runoff or following heavy summer rains. Elevated areas not subjected to flooding are dominated by white spruce (*Picea glauca*), black spruce (*P. mariana*), quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*); however, extensive areas of the marsh consist of plants that can withstand flooding such as bluejoint (*Calamagrostis canadensis*) and foxtail grass (*Alopecurus* sp.). Low-elevation areas are dominated by emergent vegetation such as horsetail (*Equisetum* sp.), mare's tail (*Hippuris vulgaris*), and pendent grass (*Arctophila fulva*). Semi-floating communities consist of moss (*Sphagnum* sp.), bog rosemary (*Andromeda polifolia L.*), and buckbean (*Menyanthes trifoliata*). Pondweed (*Potamogeton* sp.), water smartweed (*Polygonum amphibium*), and water milfoil (*Myriophyllum* sp.) dominate the submergent community.

Northern Pintails first arrive in Fairbanks between 16 and 27 April ($\bar{x}$ = 21 April), and on Minto Flats as much as one to two weeks later (Rowinski 1958). When Northern Pintails arrive, conditions on lakes may range from 100% ice cover, with no open water for feeding, to having large open areas around their edges where birds can feed. In 1987, spring thaw was delayed and all waterways, lakes, and ponds were completely frozen when birds arrived. Open water became available on the edges of large lakes within a few days, but smaller ponds were still completely ice covered in late May. Conversely, in 1988, a rapid spring thaw cleared waterways of ice and formed open-water moats around the perimeters of large lakes by the time birds arrived.

Collection of birds and body-composition analyses.—We shot birds between 28 April and 5 July in 1987 and 1988 (Table 1). We assigned females to the following reproductive categories (based partially on those proposed by Krapu 1974; terminology as per Ankney and Afton 1988): *pre-rapid follicle growth* (pre-RFG), ovary masses less than or equal to 3 g; *rapid follicle growth* (RFG), ovary masses greater than 3 g and follicles in rapid development (diameter of largest follicle ≥6.0 mm [Phillips and van Tienhoven 1962] and apparently accumulating yolk); *laying*, females in the process of laying (ruptured and developing follicles present; one female assigned to the laying category had just laid her fourth egg, had no remaining rapidly developing follicles, but had not yet developed a brood patch); *early incubation*, brood patch evident and females in first 11 days of incubation as determined by comparison with mean stage of incubation of known nests; *late incubation*, females in the last 11 days of incubation as determined by comparison with the mean stage of incubation of known nests or collected from nests where chronology was known (n = 5); *early brood rearing*, females attending ducklings less than 2.5 weeks old (class I broods; Gollop and Marshall 1954 *in* Bellrose 1980: figs. 1-5); *middle brood rearing*, females attending ducklings 2.5 to 5 weeks old (class II broods).

To estimate stage of incubation, we candled eggs (Weller 1956) in nests located during laying and incubation (n = 18 and 8 in 1987 and 1988, respectively). Ovaries were examined for presence of ruptured follicles using a 30× dissecting microscope. Females with a brood patch and developing but no apparent ruptured follicles were classified as renesters, while we defined failed nesters as females that were not attending ducklings but had brood patches that showed new feather growth. We also collected a group of females that we classified as nonbreeders. These females had regressed follicles and no evidence of ruptured follicles or a brood patch. They were collected from flocks of 6 to 10 other male and female Northern Pintails, and had average ovary (0.3 g) and oviduct masses (2.3 g) smaller than birds classed as pre-RFG (1.0 and 5.0 g, respectively). Females classified as nonbreeders, failed breeders, and renesters were analyzed separately from first-time breeders.

TABLE 1. Collection dates for Northern Pintails in each reproductive category in 1987 and 1988. Sample sizes indicated for females (F) and males (M).

Reproductive category	1987	1988
Pre-RFG	6–27 May (9F, 11M)	28 April–17 May (10F, 10M)
RFG	5 May (1F, 1M)	30 April–8 May[a] (5F, 5M)
Laying	9 May–11 June (10F, 7M)	10, 20 May (2F)
Early incubation	30 May–4 June (3F, 4M)	18 May–4 June (5F, 1M)
Late incubation	3–18 June (5F, 2M)	11–14 June (3F, 5M)
Early brood rearing	12–19 June (6F, 2M)	17–22 June (4F, 2M)
Middle brood rearing	24 June–5 July (6F, 8M)	19–25 June (4F, 1M)
Nonbreeding	10–25 June (7F, 1M)	23 May–5 June (6F, 6M)
Renesting	23 May (1F)	19–21 May (3F, 3M)
Failed breeding	—	2–8 June (2F, 1M)

[a] Two females apparently in prelaying condition (see text) were collected in 1988 on 12 and 25 May.

We collected males accompanying females when possible and assigned them to the same reproductive category as their mates. As nesting progressed and pairs broke up, we assigned males to the same reproductive status as that of most females collected during the same period. Female reproductive categories (e.g. laying or incubation) were not strictly applicable to males, but allowed us to partition the breeding season into biologically meaningful time periods.

Immediately after collection, birds were weighed to the nearest 10 g on a Pesola scale, which is referred to as fresh mass. We removed esophageal, proventricular, and gizzard contents and stored them in alcohol. We double-wrapped birds in plastic bags and froze them in the field in a portable freezer. In Fairbanks, we reweighed thawed carcasses to the nearest 0.1 g. We measured lengths of the culmen (0.1 mm), flattened wing (1 mm), diagonal tarsus (0.1 mm), keel (0.1 mm), and middle toe both with and without the nail (0.1 mm). Wing-covert markings were used to differentiate birds in their first breeding season (SY; second year) from older birds (ASY; after second year; Duncan 1985). We sheared feathers (Raveling 1979) and the shaved carcass was weighed. The heart, gizzard, liver, one-half of the breast muscle (pectoralis, supracoracoideus, and coracobrachialis), muscles of one leg (all muscles attached to the femur and tibiotarsus), and reproductive organs (left ovary and oviduct, or left testis) were removed and weighed. We stripped the ceca and the small and large intestine of their contents, then weighed and measured these organs to the nearest 1 mm. We removed all of the skin from the carcass up to the base of the skull and along the wings to the junction of the humerus with the radius and ulna. We weighed the skin as an index of subcutaneous lipid (Miller 1986). Abdominal lipid and lipid associated with the intestines also were removed and weighed.

Following dissection, each carcass was refrozen, cut into pieces, homogenized in a meat grinder, and two 30- to 40-g subsamples were removed. Liver, breast muscles, leg muscles, and reproductive tissue (ovary only) were ground and analyzed separately. We added other organs and fat depots back to the carcass before grinding, and ground samples were oven-dried to constant mass at 85°C (Kerr at al. 1982). Lipid content was determined using petroleum ether in a Soxhlet apparatus (Dobush et al. 1985). Following lipid extraction, samples were combusted in a muffle furnace at 600°C. Protein was estimated as ash-free lean dry mass. For females, we defined carcass mass as the mass of the shaved carcass minus reproductive organ mass and gastrointestinal contents. We estimated carcass lipid, protein, and ash by adding the contribution from each removed tissue (leg muscle, breast muscle, and liver) to the mean of the two carcass subsamples. We do not have estimates of lipid, protein, or ash for testes because they were homogenized with the carcass. Thus, carcass mass for males refers to the shaved carcass minus gastrointestinal contents; carcass lipid, protein, and ash include those components from the testes. All carcass estimates (water, lipid, protein, and ash) were calculated as a proportion of carcass mass as defined above for females and males.

We partitioned nutrients into nutrient reserves and nutrients committed to reproduction as in Alisauskas and Ankney (1985). That is, reproductive lipid (or protein) was estimated as lipid (or protein) in the ovary and oviduct plus the average amount of nutrient per egg times the number of ruptured follicles (Alisauskas and Ankney 1985). Nutrient reserves (lipid or protein) were defined as nutrient present in nonreproductive tissue (e. g. carcass lipid, carcass protein, carcass ash), except for males for which nutrients in the testes were included with the carcass. Four females had oviductal eggs with membranes. These were used to determine the average amount of lipid and protein per egg (5.0 and 5.5 g, respectively). We calculated lipid and protein contents of the oviduct assuming they composed 4.3 and 18.6% of the oviduct, respectively (Romanoff and Romanoff 1949). For laying females only, proportion of clutch laid was determined by dividing the number of ruptured follicles by the number of ruptured plus rapidly developing follicles.

Statistical analyses.—Data did not deviate significantly from normality for each combination of sex and reproductive category (Kolmogorov-Smirnov test; Zar 1974), so we used parametric tests. We used analysis of covariance to test for differences in carcass variables between 1987 and 1988 with Julian date as the covariate. Two-way analysis of variance (ANOVA) was used to test for variation in carcass composition by reproductive category and year, and by reproductive category and age. We used one-way ANOVA to test for differences in carcass composition among reproductive categories. If a significant result was obtained, previously planned comparisons between means of adjacent categories were made using *F*-tests (Carmer and Swanson 1973, Sokal and Rohlf 1981). To adjust for body size, we calculated the first principal-component score for each bird based on a correlation matrix of morphological variables: culmen, keel, flattened wing, middle toe, and tarsus (Alisauskas and Ankney 1987). We analyzed males and females separately. Carcass nutrients were regressed against the first principal-component score to examine the variation in these variables attributable to body size. For females, protein and ash were related to body size as

$$Y = 133 + 1.5X \quad (1)$$

for protein ($P = 0.002$), and

$$Y = 22.5 + 0.4X \quad (2)$$

for ash ($P = 0.02$), where Y is protein or ash, and X is the first principal-component score. Lipid and body size were not associated statistically ($P = 0.90$). For males, carcass protein and ash were significantly related to body size as

$$Y = 159 + 2.5X \quad (3)$$

for protein ($P = 0.001$), and

$$Y = 25.6 + 0.4X \quad (4)$$

for ash ($P = 0.02$), but lipid did not show a statistical relationship with body size ($P = 0.30$). Therefore, carcass protein and ash for females and males were corrected for body size using residuals from these regressions (as in Ankney and Afton 1988). Nine birds (four females, five males) sustained damage to a measured structure (e.g. culmen) during collection. For these birds, we used the average size of that structure for other individuals of the same sex to calculate a principal-component score.

We used multiple regression to examine depletion of protein reserves as protein was committed to reproduction. First-principal-component score (PC1) and reproductive protein were the independent variables in this analysis. We regressed lipid reserves on reproductive lipid without controlling for body size because lipid was not related to body size. We included only one RFG female in these analyses because, on the basis of size of the largest follicle, this female was one day from ovulating her first egg, while the remaining RFG females were at least four days from ovulation. We did not include all RFG birds in these regressions because our data and those of Barzen and Serie (1990: figs. 1 and 4) indicate females gain lipid and protein during RFG. Therefore, inclusion of all RFG females would cause underestimation of the slopes and Y-intercepts in regressions of nutrient reserves on reproductive nutrient (Barzen and Serie 1990).

To examine the relationship between remaining nutrient reserves and the number of additional eggs females could lay, we regressed number of rapidly developing follicles against residuals from the regression of lipid reserves (simple linear regression) and protein reserves (multiple regression) on reproductive nutrient. Residuals from the regressions of nutrient reserves on reproductive nutrients estimate the relative size of a female's nutrient reserves after controlling for commitment of nutrients to reproduction (and for protein, body size). If nutrient reserves regulate clutch size, we predict a positive association between a female's remaining nutrient reserves (residuals from regression) and the number of eggs she could still potentially lay (rapidly developing follicles).

We regressed nutrient reserves against the proportion of clutch laid to assess nutrient reserve status relative to a female's position in her own laying sequence. Finally, we tested the hypothesis that females use stored lipid reserves to help meet their energy requirements, thus freeing them to feed on less abundant proteinaceous invertebrate foods (Jones and Ward 1976, Drobney 1980, Krapu 1981). For this test, we regressed residuals from the regression of protein reserves on reproductive protein and body size, against the residuals from the regression of lipid reserve on reproductive lipid. This analysis, and the underlying hypothesis, assumes that females with larger lipid reserves at a given stage of laying can rely more heavily on these reserves to meet energy requirements, thereby reducing their requirement to meet energy needs through exogenous sources. Females with larger lipid reserves, therefore, could concentrate foraging on proteinaceous foods and use their protein reserves for egg production more slowly than females who must feed on energy-rich food. Under this hypothesis, we expect a positive association between residual protein and lipid reserves. Because of small sample sizes for our regression analyses, we used $\alpha = 0.1$ as the significance levels for our hypothesis tests to increase our power to reject the null hypothesis. All statistical procedures were performed using SYSTAT (Wilkinson 1988).

Results

Body mass and carcass-composition dynamics.—Because analysis of covariance revealed no dif-

ferences between 1987 and 1988 for any carcass variable, data from the two years were combined. We excluded two SY females from the RFG category because they were outliers (Snedecor and Cochran 1967; $P < 0.05$ that these females were from the distribution of RFG females). Both birds were classed as RFG based on ovarian condition; however, each had fresh body masses that were 200 g less than those of other RFG females (approximately equal to that of incubating females). Average carcass mass, lipid level, and protein level for these females were 533 g, 48 g, and 127 g, respectively (compare to values in Table 2 for other RFG females). It was unknown whether these birds could have produced and incubated a clutch. For completeness, however, data for RFG females are presented both with and without these birds. Carcass mass, lipid, and protein were not related to age for males or females (two-way ANOVA with age and reproductive category as factors; $P > 0.13$ in all cases); therefore, data were combined for SY and ASY birds in subsequent analyses.

Females had the greatest body mass during RFG. On average, RFG females had 45 g more lipid than pre-RFG females and 76 g more than laying females (Table 2). Average lipid content declined in each subsequent reproductive category until middle brood rearing. Average carcass protein in females declined significantly by 12 g from laying to early incubation; all other comparisons were nonsignificant.

Carcass mass of male Northern Pintails was significantly greater during the RFG period than during either pre-RFG or laying (Table 2). During the RFG period, males had 26 g more lipid than during pre-RFG and 50 g more lipid than during the laying period. No significant variation occurred in carcass protein and ash.

Average lipid levels were smaller ($P = 0.001$) for renesting females (53.3 g, Table 3) compared to RFG females (121.6 g); protein levels were similar. Levels of both lipid and protein for failed breeders were smaller than RFG and laying females. Nonbreeding females had lipid and protein levels similar to pre-RFG females.

Males in the nonbreeding, renesting, or failed nesting categories generally had lipid and protein levels similar to pre-RFG males (Table 3). However, carcass lipid levels for males collected with renesting females were the lowest of any reproductive category.

Muscle and organ dynamics.—Breast-muscle mass of females was significantly greater during RFG than during pre-RFG. Average breast-muscle mass steadily decreased from RFG through early brood rearing; declines between RFG and laying and between early and late incubation were significant ($P < 0.05$, Table 4). Leg-muscle mass increased between laying and middle brood rearing, but only the 2.6 g increase between early and middle brood rearing was significant. Lipid comprised about 1.8 g of breast muscle and 1.6 g of leg muscle during RFG, and was depleted during laying and early incubation. Changes in protein of breast and leg muscles generally paralleled changes in the respective muscle masses.

There were no significant changes in average breast-muscle mass of males, but average leg mass increased significantly between early and middle brood rearing (Table 4). Lipid associated with tissues of breast and leg muscles increased significantly before the RFG period and decreased from RFG to laying. Breast-muscle protein was greater during the RFG period than during either pre-RFG or laying periods. No significant seasonal changes in leg-muscle protein occurred in males.

No significant changes occurred in liver mass or composition for either female or male Northern Pintails (Table 5). Gizzard mass of females was at a maximum during pre-RFG, and decreased 13 g between RFG and laying. Oviduct and ovary masses increased between pre-RFG and laying; both organs regressed immediately after laying. Gizzard mass of males decreased 13 g between RFG and laying, but tended to increase after the laying period. Gut length and mass showed no significant changes. Masses of left testes averaged 7.1 g from pre-RFG through laying, and generally declined from the onset of the incubation period through early brood rearing.

Role of stored reserves in reproduction.—Lipid reserves of laying females declined significantly ($P = 0.10$) through egg laying as indicated by

$$Y = 90.8 - 2.4X, \quad (5)$$

where Y = lipid reserves and X = reproductive lipid. Regression of protein reserves of laying females on reproductive protein and PC1 scores indicated no statistical relationship between the two variables ($P = 0.23$). The equation was

$$Y = 144 - 0.22X_1 + 1.2X_2, \quad (6)$$

TABLE 2. Carcass composition (grams, mean ± SE) of female and male Northern Pintails during breeding season.

Component	Pre-RFG		RFG		Laying		Incubation				Brood rearing			
							Early		Late		Early		Middle	
Females														
n	19		6[a]		12		8		8		10		10	
Fresh mass	772 ± 16	***	876 ± 19	***	755 ± 20	ns	696 ± 26	ns	669 ± 19	ns	670 ± 18	ns	680 ± 13	
Carcass[b]														
Mass	596.4 ± 13.7	***[c]	693.2 ± 19.9	***	558.4 ± 14.6	ns	533.8 ±15.2	ns	527.7 ± 12.7	ns	520.5 ± 12.7	ns	541.2 ± 12.4	
Lipid	76.2 ± 5.8	***	121.6 ± 14.7	***	45.8 ± 8.6	ns	27.5 ± 6.5	ns	19.1 ± 3.2	ns	13.3 ± 6.1	ns	21.6 ± 4.1	
Protein	138.4 ± 3.7	ns	138.4 ± 2.6	ns	138.8 ± 2.1	*	127.1 ± 1.9	ns	125.7 ± 2.7	ns	124.5 ± 2.4	ns	128.0 ± 2.0	
Ash	23.4 ± 1.3	ns	23.8 ± 2.8	ns	23.5 ± 1.1	ns	20.8 ± 0.8	ns	22.9 ± 1.2	ns	21.5 ± 1.0	ns	20.1 ± 0.6	
Males														
n	21		6		7		5		7		4		9	
Fresh mass	906 ± 19	*	968 ± 48	*	848 ± 28	ns	932 ± 38	ns	911 ± 28	ns	901 ± 36	ns	929 ± 42	
Carcass[d]														
Mass	697.5 ± 16.0	*	779.1 ± 42.5	*	680.0 ± 23.3	ns	735.5 ± 37.1	ns	702.0 ± 20.1	ns	697.5 ± 24.3	ns	734.7 ± 33.9	
Lipid	84.2 ± 7.4	ns	109.7 ± 10.8	**	59.8 ± 9.2	ns	72.3 ± 11.5	ns	59.3 ± 12.9	ns	66.1 ± 13.7	ns	81.9 ± 11.6	
Protein	156.9 ± 3.7	ns	163.4 ± 4.9	ns	153.0 ± 4.1	ns	162.1 ± 5.0	ns	155.9 ± 3.0	ns	159.2 ± 1.6	ns	160.4 ± 6.4	
Ash	26.7 ± 1.1	ns	25.0 ± 1.4	ns	23.8 ± 0.8	ns	25.4 ± 1.4	ns	24.8 ± 1.0	ns	25.0 ± 2.2	ns	25.8 ± 0.9	

[a] Two RFG birds excluded from analyses (see text). If included, values would be as follows: $n = 8$, 826 ± 35, 650.3 ± 31.6, 102.9 ± 16.4, 134.1 ± 0.4, 22.6 ± 2.1, respectively.

[b] Carcass for females refers to shaved mass minus ovary, oviduct, and gastrointestinal contents. Where applicable, values corrected for body size.

[c] Significance level of comparisons between adjacent columns: ns indicates $P > 0.05$; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

[d] Carcass mass of males refers to shaved mass minus gastrointestinal contents. Where applicable, values corrected for body size.

TABLE 3. Carcass composition[a] (grams, mean ± SE) of female and male Northern Pintails classed as nonbreeders, failed breeders, or renesters.

Component	Nonbreeders	Failed breeders	Renesters
		Females	
n	13	2	4
Mass	593.4 ± 22.6	564.2 ± 13.6	587.4 ± 18.1
Lipid	68.4 ± 7.7	25.9 ± 1.2	53.5 ± 7.7
Protein	134.4 ± 3.3	134.5 ± 3.2	138.0 ± 2.6
		Males	
n	7	1	3
Mass	677.6 ± 20.0	718.3	673.5 ± 6.2
Lipid	70.7 ± 17.8	68.6	44.7 ± 4.5
Protein	148.7 ± 2.8	152.1	157.7 ± 0.9

[a] Carcass composition of females and males as defined in Table 2.

where Y = protein reserves, X_1 = reproductive protein, and X_2 = PC1 score. There was a significant positive relationship between number of developing follicles and the residuals from regression of protein reserves on reproductive protein (P = 0.10; Fig. 1B), but there was no significant statistical relationship between number of rapidly developing follicles and residuals from regression of lipid reserves against reproductive lipid (P = 0.32; Fig. 1A). Although no significant relationship existed between lipid reserves and the proportion of clutch laid (P = 0.69), a significant inverse relationship occurred between protein reserves and the proportion of clutch laid (P = 0.01; Fig. 2). The Y-intercept of this regression provides an estimate of the amount of carcass protein (152 g) at the beginning of laying. Finally, there was no significant relationship (n = 13, P = 0.46) between the residuals from the regression of lipid reserves on reproductive lipid and the residuals from the regression of protein reserves on reproductive protein and PC1 score.

DISCUSSION

We based criteria used to place birds into reproductive categories partially on studies by Krapu (1974), and Phillips and van Tienhoven (1962) of Northern Pintails breeding at temperate latitudes. Our definition of pre-RFG birds was based on Krapu's "arrival" category, although the entire collection period for these birds overlapped that of RFG and laying females. Although we do not know the precise chronology of arrival of Northern Pintails on Minto Flats, the last nest known to be initiated

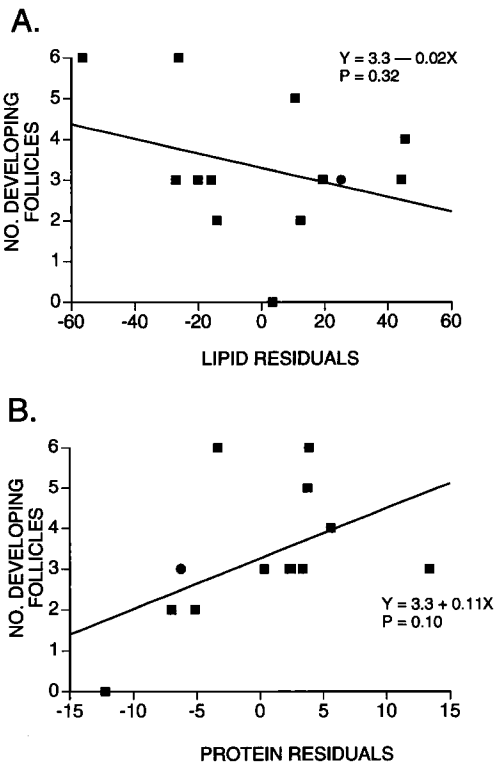

Fig. 1. Linear regression of number of rapidly developing follicles on: (A) lipid residuals (residuals from regression of lipid reserves on reproductive lipid); and (B) protein residuals (residuals from regression of protein reserves on reproductive protein and PC1 scores). Symbols indicate laying females (■) and one late RFG female (●), which were included in regression analyses.

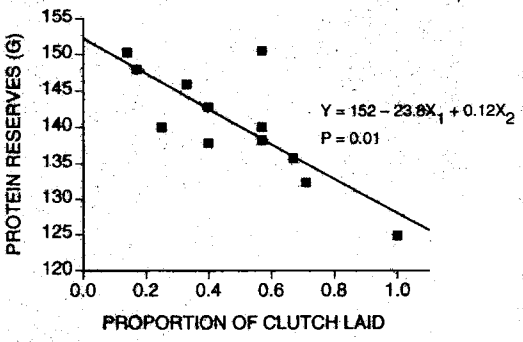

Fig. 2. Multiple regression of protein reserves (Y) on proportion of clutch laid (X_1) and PC1 score (X_2). For illustrative purposes, the third axis (PC1 score) has been deleted.

TABLE 4. Composition of one-half of the breast muscle and one leg muscle (grams, mean ± SE) of female and male Northern Pintails during breeding season. Sample sizes statistical evaluations as in Table 2.

Muscle	Pre-RFG		RFG[a]		Laying		Incubation				Brood rearing			
							Early		Late		Early		Middle	
Females														
Breast														
Mass	70.5 ± 1.6	**	79.7 ± 4.1	*	73.5 ± 1.8	ns	71.3 ± 1.9	*	64.5 ± 1.1	ns	63.4 ± 1.3	ns	66.7 ± 2.3	
Lipid	1.5 ± 0.2	ns	1.8 ± 0.5	ns	1.6 ± 0.3	*	0.4 ± 0.1	ns	0.7 ± 0.5	ns	0.2 ± 0.1	ns	0.6 ± 0.4	
Protein	17.6 ± 0.4	*	19.1 ± 1.0	ns	18.7 ± 0.4	ns	17.8 ± 0.4	***	15.3 ± 0.5	ns	14.8 ± 0.3	ns	15.9 ± 0.6	
Leg														
Mass	19.9 ± 0.6	ns	21.9 ± 0.6	ns	21.0 ± 0.4	ns	22.8 ± 0.7	ns	23.7 ± 0.3	ns	24.5 ± 0.6	**	27.1 ± 1.1	
Lipid	1.1 ± 0.1	**	1.6 ± 0.1	***	0.9 ± 0.1	*	0.5 ± 0.1	ns	0.5 ± 0.2	ns	0.3 ± 0.1	ns	0.6 ± 0.1	
Protein	4.6 ± 0.2	ns	4.9 ± 0.2	ns	4.8 ± 0.1	***	5.6 ± 0.2	ns	5.6 ± 0.1	ns	5.7 ± 0.2	*	6.2 ± 0.2	
Males														
Breast														
Mass	78.6 ± 1.6	ns	85.8 ± 3.2	ns	78.7 ± 2.6	ns	83.8 ± 2.9	ns	76.5 ± 3.5	ns	71.7 ± 4.9	ns	77.4 ± 3.4	
Lipid	1.5 ± 0.1	***	2.6 ± 0.2	***	1.2 ± 0.3	ns	1.3 ± 0.4	ns	1.2 ± 0.4	ns	1.2 ± 0.3	ns	1.3 ± 0.2	
Protein	19.8 ± 0.4	*	21.7 ± 0.6	***	19.4 ± 0.5	ns	20.5 ± 0.6	ns	18.3 ± 1.0	ns	17.9 ± 1.0	ns	18.5 ± 0.9	
Leg														
Mass	16.9 ± 0.3	ns	17.9 ± 0.8	ns	18.4 ± 0.3	ns	18.4 ± 0.6	ns	17.2 ± 0.4	ns	15.7 ± 0.8	*	18.1 ± 0.8	
Lipid	1.1 ± 0.1	*	1.6 ± 0.2	**	0.9 ± 0.1	ns	1.0 ± 0.2	ns	1.0 ± 0.2	ns	1.0 ± 0.2	ns	1.0 ± 0.3	
Protein	5.5 ± 0.2	ns	5.9 ± 0.2	ns	5.7 ± 0.1	ns	5.7 ± 0.2	ns	5.5 ± 0.2	ns	5.1 ± 0.2	ns	5.5 ± 0.3	

[a] Two RFG females excluded from analyses. If included, values would be: (breast) 76.7 ± 3.6, 1.6 ± 0.4, and 18.7 ± 0.8; (leg) 21.5 ± 0.6, 1.5 ± 0.2, and 4.8 ± 0.1.

was started on 9 June, while the last pre-RFG bird was collected on 27 May, a 13-day difference. Therefore, the last pre-RFG bird we collected could have nested within the observed nesting period on Minto Flats. Nevertheless, we do not know whether all pre-RFG birds would have eventually laid a clutch or were nonbreeders. Birds classed as nonbreeders were collected when most females on Minto Flats were incubating, and they may have represented birds displaced to the north by poor nesting conditions or drought in temperate breeding areas (see Calverley and Boag 1977, Derksen and Eldridge 1980). It is possible that some birds classed as pre-RFG could also have been displaced birds.

NUTRIENT-RESERVE DYNAMICS

Analysis of patterns.—Traditionally, use of nutrient reserves during reproduction was examined by comparing nutrient reserves of birds in different reproductive categories such as prelaying and laying (Raveling 1979, Krapu 1981, Drobney 1982, Ankney 1984, Tome 1984, Alisauskas and Ankney 1985, Hohman 1986, Ankney and Afton 1988, Barzen and Serie 1990, Afton and Ankney 1991). Recently, it was pointed out by Ankney and Afton (1988) and Alisauskas and Ankney (1992) that this approach produces conservative estimates of changes in reserve size. These authors proposed regressing nutrient reserves against nutrient devoted to reproduction to examine the role of reserves in reproduction.

The regression method is a significant advance over older techniques, but there are potential problems with the regression approach, by itself, for assessment of the role of nutrient reserves in control of clutch size. First, the regression approach assumes that individuals with different investments in reproduction at the time of collection (i.e. they have laid a different number of eggs when collected) are from the same statistical population with respect to clutch size. That is, females who have only laid two eggs when collected would have had the same mean (and variance in) clutch size, had they lived, as females that had already laid seven eggs. This assumption is unlikely to be correct in many studies because females that had already laid seven eggs at the time of collection are from a statistical population whose clutch-size distribution had a minimum value of seven eggs, whereas those females who had laid only two eggs likely were from a statistical population characterized by the entire clutch size distribution observed in nature. Therefore, all females used in regressions of nutrient reserves on reproductive nutrients may not have the same mean potential clutch size. If nutrient reserves regulate clutch size and females who have laid fewer eggs when collected would, on average, have laid smaller clutches (associated with having smaller nutrient reserves), then the regression approach will underestimate the contribution of nutrient reserves to reproduction. We examined mean expected clutch sizes for female Northern Pintails that had already laid fewer than four eggs and those that had laid four or more eggs to determine the validity of the regression approach in this study. Mean potential clutch sizes for the two groups were 6.3 and 6.2, respectively, indicating that the potential bias we discuss here was not important in our study. If nutrient reserves are correlated with clutch size, failure to account for variation in reserves at each stage of laying reduces the power of the regression approach. An additional problem of the regression method, with respect to lipid reserves, is that it cannot distinguish between: (1) the use of lipid reserves to meet energy requirements because individuals are in negative energy balance; and (2) the use of lipid for yolk production.

A better approach, we believe, is to control for stage-of-laying using the residuals from the regression of nutrient reserves on reproductive nutrient, and where appropriate, PC1 scores. If nutrient reserves regulate clutch size, then the number of rapidly developing follicles should be positively correlated with residual nutrient reserves. Females that have larger nutrient reserves after controlling for the number of eggs already laid should have a larger number of developing follicles if nutrient reserves directly control clutch size. This approach should be restricted to females late in laying for most species of ducks because a maximum of about six rapidly developing follicles can be detected in the ovary (Ankney and Afton 1988).

Ankney and Afton (1988) used a similar approach when they regressed number of rapidly developing follicles against lipid reserves for female Northern Shovelers that had already laid five eggs. These authors interpreted the positive correlation they observed as evidence in support of the hypothesis that lipid reserves regulate clutch size in Northern Shovelers. Females with a larger number of rapidly

TABLE 5. Organ size (grams, except gut length is in mm; mean ± SE) for female and male Northern Pintails. Due to tissue damage during collection, sample sizes that differ from those in Table 2 are indicated in parentheses.

Component	Pre-RFG		RFG[a]		Laying		Incubation				Brood rearing			
							Early		Late		Early		Middle	
Females														
Liver	11.8 ± 0.9	ns[b]	13.6 ± 1.1	ns	12.4 ± 0.8	ns	10.9 ± 0.7	ns	11.1 ± 0.9	ns	11.9 ± 0.6	ns	11.9 ± 0.5	
Gizzard	31.7 ± 1.4 (18)	ns	31.0 ± 1.4	***	17.7 ± 1.0	ns	21.3 ± 2.8	ns	20.2 ± 2.5	ns	21.3 ± 2.5	ns	24.4 ± 2.5	
Oviduct	6.6 ± 0.6 (18)	ns	9.2 ± 1.4	***	26.0 ± 4.4	***	2.9 ± 0.8 (7)	ns	1.6 ± 0.2 (6)	ns	1.3 ± 0.2	ns	0.8 ± 0.2	
Ovary	0.7 ± 0.1	**	4.0 ± 1.0	***	10.1 ± 1.7	***	0.3 ± 0.1	ns	0.2 ± 0.1	ns	0.2 ± 0.1	ns	0.1 ± 0.1	
Gut	18.4 ± 1.7 (15)	ns	15.9 ± 1.2	ns	15.6 ± 1.2	ns	16.4 ± 1.3 (7)	ns	25.0 ± 1.8 (6)	ns	22.5 ± 1.0	ns	21.8 ± 1.0	
Gut length	1,781 ± 48	ns	1,658 ± 67	ns	1,549 ± 73	ns	1,762 ± 74	ns	1,802 ± 65	ns	1,795 ± 37	ns	1,706 ± 39	
Males														
Liver	12.3 ± 1.0 (19)	ns	13.6 ± 1.6	ns	16.2 ± 1.9	ns	14.7 ± 1.9	ns	13.9 ± 1.5	ns	14.8 ± 0.7	ns	17.1 ± 1.4	
Gizzard	32.6 ± 2.0 (20)	ns	37.0 ± 4.9	*	24.0 ± 1.9	ns	31.8 ± 3.7	ns	39.3 ± 2.6	ns	43.8 ± 8.4	ns	36.1 ± 4.0	
Testes	7.3 ± 1.0 (14)	ns	5.8 ± 1.2	ns	8.1 ± 1.6	ns	4.9 ± 2.7 (4)	ns	1.5 ± 1.0	ns	0.4 ± 0.3	ns	0.3 ± 0.1	
Gut	18.5 ± 1.3 (12)	ns	20.8 ± 4.1	ns	19.5 ± 2.4	ns	22.9 ± 3.1	ns	28.7 ± 2.0	ns	29.1 ± 2.9	ns	29.9 ± 2.3	
Gut length	1,834 ± 47 (12)	ns	1,850 ± 112	ns	1,775 ± 59	ns	1,916 ± 71	ns	2,020 ± 52	ns	2,008 ± 85	ns	2,057 ± 52	

[a] Two RFG females deleted. If included, values within table would be: 12.9 ± 1.0, 29.1 ± 3.6, 9.2 ± 1.5, 3.9 ± 0.9, 14.6 ± 1.7, and 1,331 ± 34.9.

[b] As in Table 2.

developing follicles are likely to be found earlier in their own laying period, however, and the positive correlation could have resulted from females earlier in laying having both larger lipid reserves and more rapidly developing follicles. Regression of number of rapidly developing follicles against residuals from the nutrient reserve-reproductive nutrient regression avoids the confounding effect of stage of laying by controlling for this variable.

Lipid dynamics.—Our results suggest that female Northern Pintails nesting in subarctic Alaska accumulated lipids before arrival. Lipid also increased after arrival but before egg laying; females reached their peak mass during RFG and subsequently used these reserves during laying, early incubation, and brood rearing. Our finding is similar to those of studies showing that female ducks store lipids before (Krapu 1981), or after (Drobney 1982, Tome 1984, Hohman 1986, Barzen and Serie 1990) arrival on breeding areas. These lipid reserves are then used to meet energy and potentially lipid requirements during laying and incubation.

Table 2 indicates that female Northern Pintails lost an average of 94 g of lipid from RFG to early incubation, which we recognize is a conservative estimate of lipid loss during egg laying (Alisauskas and Ankney 1992). Nevertheless, because an average clutch of 6.7 eggs (mean of 26 clutches found in 1987 and 1988) contained 34 g of lipid, at least 1.8 g of lipid were used to meet maintenance energy requirement for each gram of lipid deposited in eggs.

An alternative method for estimating loss of lipid reserves is to use the slope of the regression line of lipid reserves on reproductive lipid. This method indicates female Northern Pintails lost 2.4 g of lipid for each gram devoted to reproduction, which may underestimate rate of lipid loss (see above). Therefore, at least 1.4 g of lipid were required to meet maintenance energy requirements for each gram required for reproduction. Our results contrast with those for other Anatini and Aythini, in which declines in lipid reserves during egg laying never exceeded, and were usually less than, lipid devoted to reproduction (Krapu 1981, Ankney and Afton 1988, Alisauskas et al. 1990, Afton and Ankney 1991, Ankney and Alisauskas 1991, Alisauskas and Ankney 1992). Barzen and Serie (1990) also observed use of lipid reserves to meet maintenance energy requirements in female Canvasbacks; however, female Northern Pintails depleted lipid reserves approximately 1.3 times faster than did Canvasbacks.

Male Northern Pintails are not highly territorial, but they form weak pair bonds and accompany their mates during the RFG and laying periods (Derrickson 1978). Increased energy expenditure associated with activities such as pursuit flights, courtship displays, and mate defense (Smith 1968, Derrickson 1978), and/or a decrease in the time spent feeding (Dwyer 1975, Afton 1979) may account for the decrease in lipid between the RFG and laying periods. Dissolution of pair bonds early in incubation (Sowls 1955) may then allow males to restore depleted lipid reserves.

Male and female Northern Pintails leave California in March weighing approximately 1,030 and 900 g, respectively (Miller 1986). Because California is the likely wintering area for many Northern Pintails breeding in Alaska (Bellrose 1980), these masses provide a reasonable baseline against which to compare masses of Northern Pintails in Alaska. Male and female Northern Pintails classified as pre-RFG weighed approximately 120 and 130 g less, respectively, than birds prior to departure from California (Miller 1986). Virtually all of this loss can be accounted for by carcass lipids, which were 120 and 115 g lower in males and females classed as pre-RFG at Minto Flats compared to Northern Pintails in California prior to migration. These data suggest that lipid reserves deposited in winter play an important role in migration. Because birds arrive with lipid reserves and use those reserves plus lipid accumulated on Minto Flats during reproduction, lipid reserves accumulated on the wintering grounds or staging areas also may play an important role in reproduction of Northern Pintails. These results are consistent with analyses of Raveling and Heitmeyer (1989), who showed that winter habitat conditions in California may influence reproductive success of Northern Pintails the following breeding season.

Protein dynamics.—Our estimate of the rate of depletion of protein reserves in relation to reproductive protein was imprecise (owing to variation in protein reserves and our relatively small sample) and was estimated as a loss of approximately 0.22 g of protein reserve for each gram devoted to reproduction. Changes in mean nutrient level between laying and early incubation (Table 2) conservatively estimated a 12-g decrease in protein reserves during egg laying

(assuming protein reserves did not change after the birds began incubation). However, this is an underestimate of the true loss because 10 of 12 laying females had already laid at least two eggs. We estimate that females began laying with 152 g of protein (Fig. 2, *Y*-intercept; 95% confidence limits were 143 to 160 g, depending on body size) and ended laying with 128 g of protein. Thus, females lost approximately 23 g of protein (range 15 to 32 g). To fulfill protein requirements for an average clutch (37 g), and assuming a conversion efficiency from endogenous protein to egg protein of 96 to 100% (Alisauskas and Ankney 1985, Sturkie 1986), the above estimates of carcass protein loss during laying indicate that carcass protein could have provided between 21 and 62% of the protein required for egg production.

Possible sources of endogenous protein for egg production are the digestive tract and musculature. Average gut length and mass showed no significant changes between adjacent periods and, although both tended to decline from pre-RFG to laying, the differences were not significant ($P = 0.11$ and 0.06 for the two measures, respectively). However, gizzard protein could have contributed about 3.5 g (9%) to the protein requirement for egg production in female Northern Pintails, which is less than has been observed in Common Eiders (ca. 20 g or 38%; Korschgen 1977), but proportionally similar to estimates for Cackling Canada Geese (*Branta canadensis minima*; ca. 6 g or 8%; Raveling 1979). Reduction in gizzard size was not associated with a dietary shift in Northern Pintails (Burris 1991) and, therefore, was not likely a result of reduced food or fiber intake as has been described in other species (Miller 1975, Krapu 1981, Drobney 1982, Kehoe et al. 1988). We detected only minor changes in breast- and leg-muscle size between RFG and incubation. These results are consistent with other studies of breeding ducks (Krapu 1981, Drobney 1982, Reinecke et al. 1982, Ankney and Afton 1988), and contrast with those of geese in which muscle tissues contribute substantially to the protein requirements for breeding (Ankney and MacInnes 1978, Raveling 1979). It is likely that protein was lost from the gizzard, gut, and skeletal musculature, but possibly significant changes in individual tissue were below our ability to detect them.

Males showed little variation in the size of protein stores, with the exception of the gizzard. Gizzard mass decreased 35% between RFG and laying. This decrease may have been associated with reduced time spent feeding during their mates' laying period (Burris 1991).

Control of clutch size.—Ankney and Afton (1988) proposed that the ability of female Northern Shovelers (and possibly other species of ducks) to synthesize lipids limited egg production. Their hypothesis was based on the decline in lipid reserves as laying progressed, the predominance of protein relative to lipid in Northern Shoveler diets, and on the relationship between number of rapidly developing follicles and remaining lipid reserves for females late in laying. These observations do not by themselves distinguish between the role of lipid, per se, versus the role of energy (of which lipid is an important source) in limiting egg production.

Our data do not support the hypotheses that either lipid or energy limits clutch size in Northern Pintails. However, lipid clearly plays an important role in the reproduction of Northern Pintails, as evidenced by the relatively large lipid reserves present in pre-RFG birds, and subsequent increases in these reserves before laying. While lipid levels declined during egg laying, we observed no relationship between lipid reserves and proportion of the clutch laid. Also, there was no relationship between residual lipid reserves (controlling for investment in reproduction) and remaining number of rapidly developing follicles. Barzen and Serie (1990) also observed declining lipid reserves with increasing investment in a clutch. Nevertheless, their data are inconsistent with the lipid-limitation hypothesis because lipid reserves were increasing coincident with the beginning of maximum daily lipid requirement for egg production (the day before laying the first egg; Alisauskas and Ankney 1992). They attributed declines in lipid reserves to negative energy balance as laying progressed, owing to increased nest attentiveness and reduced foraging time during laying. We believe this also best describes the situation in Northern Pintails. Additionally, we speculate that lipid reserves also could have influenced reproductive success by affecting nest attentiveness during incubation (Sherry et al. 1980, Aldrich and Raveling 1983, Ankney and Alisauskas 1991, Gloutney and Clark 1991) or brood attentiveness.

Several lines of evidence indicate that clutch size in Northern Pintails is regulated in part by the size of endogenous protein reserves. Pro-

tein reserves declined during egg laying, and protein reserves that remained at a given stage of laying were negatively related to the proportion of clutch laid. Predicted protein levels at completion of laying (Fig. 2) were comparable to observed protein levels in incubating females, suggesting that a minimum protein threshold exists that terminates laying, as has been suggested for Cackling Canada Geese (Raveling 1979). The number of rapidly developing follicles was positively related to residual protein reserves (i.e. females with larger protein reserves at each stage of laying had more remaining developing follicles). This may suggest that the potential clutch size of females was somehow adjusted to match the size of a female's prelaying protein reserve, which is analogous to the use of nutrient reserves in Lesser Snow Geese (*Chen caerulescens caerulescens;* Ankney and MacInnes 1978).

The extent to which female Northern Pintails can complement protein reserves with dietary protein will reduce the need to use protein reserves to produce each egg. Many species of ducks such as Gadwalls (Serie and Swanson 1976, Ankney and Alisauskas 1991), Mallards (Swanson et al. 1979), Wood Ducks (Drobney 1982), Ruddy Ducks (*Oxyura jamaicensis;* Tome 1984), Ring-necked Ducks (*Aythya collaris;* Hohman 1985), Redheads (*A. americana;* Noyes and Jarvis 1985), and Canvasbacks (*A. valisineria;* Noyes and Jarvis 1985) increase invertebrate consumption during the breeding season. Our data indicate a large proportion of protein in a Northern Pintail clutch in the subarctic is supplied by previously stored reserves, which is associated with the lack of increased consumption of invertebrates during laying in these females (Debruykere 1988, Burris 1991). This is consistent with the prediction (Ankney and Afton 1988, Ankney and Alisauskas 1991) that if females had difficulty obtaining exogenous protein during egg production, they would store and use protein. This has been observed in at least some early-nesting female Ring-necked Ducks (Alisauskas et al. 1990) and breeding Gadwalls (Ankney and Alisauskas 1991).

It has also been hypothesized that lipid reserves play an indirect role in the protein budget of females during egg production by allowing females to spend time foraging for food with high protein content (Jones and Ward 1976, Drobney 1980, Krapu 1981). If this was the case for female Northern Pintails, we would expect females with the largest lipid reserves at each stage of laying to also have the largest protein reserves. Under this hypothesis, females with larger lipid reserves at each stage of laying could rely more heavily on their reserves to meet maintenance requirements than females with smaller lipid reserves, thereby allowing them to concentrate foraging on proteinaceous foods. Greater intake of dietary protein would require less protein from nutrient reserves for production of each egg. Females with larger lipid reserves who could spend more time feeding on invertebrates, therefore, would conserve protein reserves. Our data do not support this hypothesis, as there was no relationship between size of residual protein and lipid reserves in female Northern Pintails after correcting for stage of laying.

In summary, storage of protein before arrival on breeding areas suggests that nutrient dynamics in Northern Pintails represent a strategy for early breeding (i.e. it allows initiation of egg laying before proteinaceous foods are abundant), as in arctic-nesting geese. Lipid stored before breeding is also important because females are in negative energy balance during egg laying and incubation. Our data suggest that nutrient acquisition on wintering areas may be important to nesting success for Northern Pintails in subarctic Alaska, which is consistent with the finding of Raveling and Heitmeyer (1989) that winter habitat conditions are positively correlated with the production of young in the next breeding season. Unfortunately, comparable data do not exist for Northern Pintails nesting in temperate regions, so we cannot determine whether differences between our results and those of others are phylogenetically or geographically based (i.e. whether the dynamics of nutrient reserves we observed are characteristic of Northern Pintails or of ducks breeding at high latitudes). Comparative studies of mid- and high-latitude populations of the same species are necessary to resolve these issues.

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