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NUTRIENT RESERVES AND CLUTCH-SIZE REGULATION OF NORTHERN SHOVELERS IN ALASKA

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ABSTRACT.—We determined patterns of nutrient-reserve use by female Northern Shovelers (*Anas clypeata*) nesting at Minto Flats, Alaska, and compared them with those of female shovelers nesting in the Prairie Pothole Region of Manitoba, Canada. Individual variation in somatic lipid was best explained by nest initiation date; females that initiated nests early had larger lipid reserves than females that delayed nest initiation. These results contrast with those from Manitoba, which showed that females used lipid reserves and stored protein during egg production. Incubating females from Alaska did not use protein or mineral reserves, but lipid reserves decreased significantly throughout incubation. Females in Alaska and Manitoba used lipid reserves similarly during incubation. We conclude that endogenous nutrient availability does not proximately limit clutch size during laying for this population of shovelers, possibly due to the high productivity of wetlands in interior Alaska and/or the long photoperiod that allow females to forage extensively. Successful completion of incubation or brood rearing may be an ultimate factor that controls clutch size for this population of shovelers. *Received 17 May 1999, accepted 28 April 2000.*

LACK (1967) proposed that for species with precocial young, mean clutch size is determined by the average amount of nutrients available to females at the time of egg production. Ryder (1970) modified Lack's (1967) hypothesis to accommodate species such as arctic-nesting geese, which rely heavily or exclusively on endogenous reserves as a source of nutrients for egg production. Most ducks of the genus *Anas*, having a smaller body size than geese, are not capable of storing sufficient body reserves to produce an entire clutch (Afton and Paulus 1992). Accordingly, such species often use a combination of nutrient reserves and exogenous food to supply remaining nutrients for clutch completion (Alisauskas and Ankney 1992).

Use of somatic nutrients by female waterfowl during egg production has been interpreted as evidence that females cannot acquire sufficient quantities of these nutrients in their daily diets (Ankney et al. 1991), potentially limiting clutch size. Nearly all studies of temperate-nesting ducks have detected use of lipid reserves during egg laying (Afton and Ankney 1991, Ankney and Alisauskas 1991, Young 1993). Although several studies have detected use of protein reserves by laying females (Ankney and Alisauskas 1991, Mann and Sedinger 1993, Esler and Grand 1994), in most cases protein was not used at as high a rate as lipid. Use of lipid reserves, combined with a positive relationship between the number of rapidly developing follicles in the ovary and the amount of remaining somatic lipid, has been interpreted as support for the hypothesis that lipid reserves limit egg production in these species of ducks (Alisauskas and Ankney 1992).

Most studies of nutrient reserves in ducks have been conducted in the prairies of North America (e.g. Krapu 1981, Tome 1984, Ankney and Alisauskas 1991). Only two such studies, both of Northern Pintails (*Anas acuta*), have been conducted on high-latitude populations outside the prairies (Mann and Sedinger 1993, Esler and Grand 1994), but nutrient-reserve use has not been studied in this species within the prairies. Thus, it has not been possible to assess the generality of patterns of nutrient-reserve dynamics in duck populations outside the prairie region because comparable data are lacking.

Subarctic-nesting ducks may have greater difficulty than prairie-nesting ducks in meeting energy and nutrient requirements during egg production. First, ducks nesting at high latitudes migrate relatively farther from their wintering grounds than do temperate-nesting

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ducks, using more energy during migrations. Second, the time available for egg production and brood rearing is reduced because of the shortened season at high latitudes. Therefore, females may not have enough time to replenish nutrients after arrival on the breeding grounds.

The purpose of our study was to investigate patterns of nutrient-reserve use by Northern Shovelers (*Anas clypeata*; hereafter "shovelers") breeding in a subarctic wetland and to compare our results with data for shovelers breeding in Manitoba (Ankney and Afton 1988). If exogenous nutrients limit egg production in shovelers nesting in Alaska, we predicted we would observe similar or higher use of nutrient reserves by Alaskan shovelers compared with those nesting in Manitoba (Ankney and Afton 1988).

METHODS

Our study was conducted on the Minto Flats State Game Refuge (64°50'N, 148°50'W) in central Alaska during the summers of 1991 to 1993 (see Mann and Sedinger [1993] for a description of the study area). On average, shovelers begin to arrive at Minto Flats on 28 April, and they initiate nests from mid-May to mid-June (Petrula 1993).

Body composition.—We shot females beginning mid-May in each year (ca. two weeks before peak nest initiation) and continued collecting birds until most females on the study area had begun incubation. Each day, we started at a randomly chosen location on the study area and opportunistically collected females as they were encountered. We collected randomly chosen females on nests late in laying and during incubation to complete the sample of breeding birds. When collected, we weighed females with a Pesola scale (±10 g) and measured the following morphological characters (±0.1 mm) using vernier calipers: keel, culmen length, culmen width at the widest point, body length from distal edge of culmen to end of pygostyle, wing chord, and tarsus. We removed the ovaries and oviducts upon collection and placed them in 10% formalin. The remaining carcass was double-wrapped in plastic bags and frozen for later analysis.

We classified females into one of four reproductive categories (non-rapid follicle growth, rapid follicle growth, laying, or incubating; Ankney and Afton 1988). Females whose follicles contained no yolk and who had not initiated rapid follicle growth were classified as "non-rapid follicle growth" (non-RFG). Females with at least one yolky follicle with a dry mass more than 0.1 g but with no postovulatory follicles were classified as "rapid follicle growth" (RFG), whereas females that had at least one postovulatory follicle and one or more follicles in rapid development were classified as "laying" (Ankney and Afton 1988). "Incubating" females were collected from nests whose age was known based on candling of eggs (Weller 1956).

In the laboratory, we shaved and plucked carcasses to remove all feathers (Raveling 1979). Intestinal tracts were removed, weighed, stripped of their contents, and then reweighed. The gizzard also was excised and weighed, cleaned of its contents, and reweighed. Carcasses, with all organs replaced, were homogenized in a meat grinder three times, and two approximately 30-g aliquots were removed for compositional analyses. We dried aliquots at 90°C to constant mass, extracted lipid from aliquots with petroleum ether using a Soxhlet apparatus (Dobush et al. 1985) for 24 h, and determined mineral content by combusting samples in a muffle furnace (Ankney and Afton 1988). The two aliquots from each female were not analyzed at the same time during any procedure, so variation in aliquot composition was indicative of how well carcasses were homogenized and the consistency of our laboratory procedures.

We estimated protein content of aliquots as the difference between dried, lipid-free aliquot mass and mineral mass. We calculated somatic lipid (S-lipid), somatic protein (S-protein), and somatic mineral (S-mineral) by multiplying the proportions of each nutrient in aliquots by the ingesta-free and feather-free carcass mass (Ankney and Afton 1988). We assessed our percent measurement error (see Lessells and Boag 1987, Lougheed et al. 1991) in extracting nutrients from the two aliquots from each carcass using PROC NESTED (SAS 1992). Percent measurement error was calculated as: $[s^2_{\text{within carcasses}}/(s^2_{\text{among carcasses}} + s^2_{\text{within carcasses}})]$. For this analysis, we used data from all carcasses analyzed for nutrient content.

Reproductive organs.—Ovaries from non-RFG birds were kept intact and analyzed for lipid, protein, and mineral content using the procedures described above. For laying birds, each yolky follicle was excised and analyzed separately (Ankney and Afton 1988), and the remaining portion of the ovary also was analyzed. We assumed that follicles damaged during collection had the same nutrient content as follicles at the same stage of development in a sample of birds with a complete set of developing follicles (Afton and Ankney 1991). To estimate the nutrient content of damaged follicles, we regressed the mass of nutrient from the largest follicle on the mass of nutrient in the next-largest follicle in the hierarchy. Corrective equations were: $\text{fat}_{\text{follicle}} = 1.5517 + 0.9838 \times \text{fat}_{\text{follicle}-1}$ ($n = 8$, $r^2 = 0.77$) and $\text{protein}_{\text{follicle}} = 0.10206 + 0.6334 \times \text{protein}_{\text{follicle}-1}$ ($n = 8$, $r^2 = 0.68$).

Oviducts were removed from formalin, rinsed thoroughly, dried, and analyzed for nutrient content. To estimate nutrients committed to eggs by laying and incubating females, we collected 32 unincubated eggs from nests located while nest searching each

summer and determined average lipid, protein, and mineral content. Mean values for these eggs were 5.19 ± SE of 0.05 g lipid, 5.01 ± 0.04 g protein, and 3.15 ± 0.05 g mineral. Egg protein was calculated as (mean yolk lean dry mass + mean dry albumen; Ankney and Afton 1988). We multiplied the number of postovulatory follicles in ovaries of laying and incubating females by the average mass of nutrients found in the sample of unincubated eggs. We added all components of the reproductive tract plus eggs already laid to determine total nutrient commitment to reproduction (R-lipid, R-protein, and R-mineral).

Statistical analyses.—To control for variation in structural size among birds, we computed principal component scores for each bird (Alisauskas and Ankney 1987) based on a correlation matrix of wing chord, tarsus length, and body length. These measurements were the most highly correlated with S-protein and thus would best describe structural size of females (D. Ankney pers. comm.). The first principal component (PC1) had an eigenvalue of 1.36 and was positively correlated with all three morphological measurements (loadings ranged from 0.44 to 0.68). PC1 explained 45% of the total variance in the measurement data and was included in subsequent analyses as a measure of body size.

To control for annual variation in laying date among females, we calculated standardized nest initiation dates in each year for laying and incubating females. Using known-age nests (110 in 1991, 105 in 1992, and 112 in 1993), we determined the dates on which the highest numbers of nests were initiated (i.e. peak initiation date) and assigned that date a value of 0. Females that did not initiate nests on the peak were assigned a negative or positive value equal to the number of days that they started laying before or after the peak initiation date.

To evaluate the contribution of each somatic nutrient (S-lipid, S-protein, and S-mineral) made to reproduction, we used models in which somatic nutrient was the dependent variable and the independent variables were reproductive nutrient, year, standardized nest initiation date, PC1, and all possible two-way interactions. The contribution of each variable was evaluated using type III sums of squares. Interaction terms that did not contribute significantly ($P > 0.05$) to the model were sequentially eliminated in a backward manner. The model was run for RFG and laying birds only because non-RFG birds may not have initiated nests. We conducted a separate analysis for incubating birds that included day of incubation as a continuous variable, rather than R-nutrient. For all analyses, we excluded females thought to be renesters ($n = 8$) based on a combination of macroscopic and microscopic inspection of ovaries (Arnold et al. 1997).

We also used the method of Sedinger et al. (1997) to directly test the hypothesis that nutrient reserves regulated clutch size. This analysis was restricted to females late in laying for whom potential clutch size could be determined. Late layers were classified as females with at least five postovulatory follicles and at least one RFG follicle. We used an ANCOVA with S-nutrient (protein, lipid, and mineral) as the dependent variable, calculated clutch size as a class variable, (no. of postovulatory follicles + no. of RFG follicles), and standardized date of nest initiation and R-nutrient as covariates. A significant effect of clutch size is evidence of nutrient limitation of clutch size (Sedinger et al. 1997).

To assess geographic differences in S-lipid, S-protein, and S-mineral use by females during egg production and to make direct comparisons between Alaska and Manitoba, we obtained the original Manitoba data from Ankney and Afton (1988) and analyzed the two data sets in the same manner. We calculated a PC1 score for these females by first determining which measurements were the most correlated with S-protein and found that for Manitoba females those measurements were culmen length, bill height, and stripped keel length ($r = 0.31$ to 0.46, $P = 0.02$ to 0.0004). Using those three measurements for the 55 RFG/laying females, PC1 explained 44% of the total variance, had an eigenvalue of 1.31, and had positive factor loadings that ranged from 0.72 to 1.31.

Date of nest initiation had not been calculated for the Manitoba data set, so we determined a standardized date of RFG initiation for Alaska and Manitoba females in the same manner used to calculate standardized date of nest initiation for the Alaska data set, except that we used the peak day of RFG initiation as day 0. We first analyzed the S-nutrients for pre-RFG/RFG and laying Manitoba females in the same manner as for Alaska females (see above). To compare rates of nutrient use during egg production, we used PROC GLM and a model with S-nutrient as the dependent variable; area of collection (Alaska or Manitoba) as a class variable; R-nutrient, body size, and standardized date of RFG initiation as covariates; and the interaction of R-nutrient × area. To compare incubating birds, we used a model of S-lipid as the dependent variable, day of incubation as a covariate, area of collection as a class variable, and the interaction of day of incubation × area. Estimates of all parameters are reported as $\bar{x} \pm$ SE.

Results

Collection.—We collected 46 female shovelers in 1991, 30 in 1992, and 24 in 1993. Collection dates ranged from 20 May to 3 July in 1991, 19 May to 14 July in 1992, and 18 May to 13 July in 1993. The peak dates of nest initiation were 29 May 1991, 28 May 1992, and 27 May in 1993. The range over which incubating birds were

TABLE 1. ANCOVA results describing variation in nutrient reserves for RFG (rapid follicle growth) and laying female Northern Shovelers at Minto Flats, Alaska. Nest initiation date was standardized within each year.

Model								
Dependent variable	F	P	r^2	Intercept[a]	Source	Estimate[a]	F	P
S-lipid (n = 41)	1.92	0.14	0.13	49.96 ± 4.77	R-lipid	−0.02 ± 0.17	0.02	0.88
					Body size	1.83 ± 2.53	0.53	0.47
					Nest initiation date	−0.76 ± 0.32	5.75	0.02
S-protein (n = 41)	2.40	0.08	0.16	108.84 ± 3.18	R-protein	0.13 ± 0.10	1.80	0.18
					Body size	−0.46 ± 1.52	0.09	0.77
					Nest initiation date	0.42 ± 0.19	4.96	0.03
S-mineral (n = 41)	5.15	0.002	0.36	18.96 ± 2.35	R-mineral	−0.19 ± 0.12	2.79	0.10
					Body size	2.12 ± 0.91	5.40	0.03
					Nest initiation date	−0.09 ± 0.11	0.68	0.41
					Year		26.75	0.001

[a] Parameter estimate ± 1 SE.

collected was day 3 to 18 in 1991, day 1 to 23 in 1992, and day 4 to 24 in 1993.

Body mass and measurement error.—The average fresh body mass of collected females was 575.5 ± 9.5 g. The combined wet mass of both aliquots analyzed from each carcass averaged 57.62 ± 1.06 g, and the dry mass averaged 19.06 ± 0.37 g. Our percent measurement error within aliquots from each female was 11.8% for lipid, 11.6% for protein, and 10.9% for mineral.

Egg production.—For RFG and laying birds combined (n = 41), lipid reserves declined 0.76 g for each day of delay in nest initiation (Table 1). No other variables or interactions we tested in the lipid model were significant ($P > 0.05$). The point estimate for R-lipid was −0.02, which indicated that nutrient reserves contributed approximately 2% of the total lipids required for egg laying, an amount that was highly nonsignificant (P = 0.88). In addition, we found no evidence of collinearity between R-lipid and standardized date of nest initiation (r^2 = 0.003, n = 41, $P > 0.05$).

In contrast to S-lipid, the relationship between S-protein and standardized nest initiation date was positive, with S-protein increasing 0.42 g for each day of nest initiation (Table 1). S-protein increased by an average of 0.13 g for every g of protein devoted to reproduction, but this relationship was not significant (P = 0.18). We observed annual variation in S-mineral for our sample of birds, and S-mineral also increased with body size (Table 1). S-mineral declined by 0.19 g for every gram devoted to egg production, but this result was not quite significant (P = 0.10; Table 1). Assuming that this relationship was real, mineral reserves would have contributed enough calcium for about two eggs in a typical 10-egg clutch.

For the 14 laying females that had laid five or more eggs and had one or more developing follicles (late layers), S-lipid was not related to potential clutch size (F = 0.48, df = 4 and 7, P = 0.75), R-lipid (F = 0.21, df = 1 and 7, P = 0.66), or standardized date of nest initiation (F = 0.21, df = 1 and 6, P = 0.66). Nor did clutch size explain a significant amount of variation in S-protein (F = 1.09, df = 4 and 7, P = 0.43). Neither R-protein (F = 2.83, df = 1 and 7, P = 0.14) nor standardized date of nest initiation (F = 0.00, df = 1 and 7, P = 0.96) explained significant variation in S-protein. Similarly, variation in S-mineral for late layers was not explained by clutch size (F = 0.65, df = 1 and 7, P = 0.65), R-mineral (F = 1.01, df = 1 and 7, P = 0.34), or standardized date of nest initiation (F = 0.21, df = 1 and 7, P = 0.66).

Incubation.—Variation in somatic lipid for incubating females (n = 38) was best described by a model that included day of incubation and standardized date of nest initiation. On average, lipid reserves declined by 1.01 ± 0.37 g for each day of incubation (F = 8.04, df = 1 and 35, P = 0.007) and by an additional 0.86 ± 0.30 g for each day later that the nest was initiated (F = 11.45, df = 1 and 35, P = 0.001). Somatic protein declined with nest initiation date (b = −0.41 ± 0.17 g day^{-1}; F = 5.85, df = 1 and 35, P = 0.02) but was unaffected by days spent incubating (F = 0.06, df = 1 and 35, P = 0.81). S-mineral of incubating females varied by year (F = 10.69, df = 1 and 33, P = 0.003) but was un-

affected by standardized date of nest initiation ($F = 1.08$, df = 1 and 33, $P = 0.31$) or day of incubation ($F = 0.64$, df = 1 and 33, $P = 0.43$).

Geographic variation in egg production and incubation.—One main goal was to analyze the Alaska and Manitoba data sets in the same manner so that results were directly comparable. For the Manitoba data set, date did not explain variation in S-lipid ($F = 2.54$, df = 1 and 51, $P = 0.12$), and S-lipid was used at a significant rate during egg production ($F = 19.77$, df = 1 and 51, $P < 0.001$; $b = -0.73 \pm 0.16$ g S-lipid * g R-lipid^{-1}). For S-protein, only body size explained variation in S-protein ($F = 18.48$, df = 1 and 51, $P < 0.001$). Although R-protein was not significant in the model, the slope estimate was in the same direction as Ankney and Afton (1988) reported ($b = 0.05 \pm 0.04$ g S-protein * g R-protein^{-1}). Variation in S-mineral was explained by standardized date of RFG initiation ($F = 5.69$, df = 1 and 51, $P = 0.02$) and body size ($F = 9.55$, df = 1 and 51, $P = 0.003$). S-mineral increased 0.14 ± 0.06 g for each day delay in RFG initiation.

In comparing rates of use/storage of nutrients between Alaska and Manitoba females, S-lipid declined during egg production. S-lipid declined during egg production for Manitoba females but did not change for Alaska females (Fig. 1); these differences in slope were significant ($F = 11.24$, df = 1 and 90, $P = 0.001$). The y-intercept for Alaska females was 15.10 ± 5.73 g lower than that for Manitoba females ($F = 6.93$, df = 1 and 90, $P = 0.01$; Fig. 1).

Slopes of the lines representing S-protein dynamics for Alaska and Manitoba shovelers did not differ ($F = 0.01$, df = 1 and 90, $P = 0.91$); however, the adjusted y-intercept of Alaska females was 13.13 ± 3.01 g above the y-intercept for Manitoba females ($F = 19.01$, df = 1 and 90, $P < 0.001$; Fig. 1). Slopes of lines describing changes in S-mineral with R-mineral differed between Alaska and Manitoba ($F = 8.71$, df = 1 and 90, $P = 0.004$) because Alaska females used S-mineral to produce R-mineral, whereas Manitoba females did not use S-mineral in egg production. In addition, the y-intercept of Alaska birds was 4.98 ± 1.34 g above the Manitoba intercept ($F = 13.91$, df = 1 and 90, $P < 0.001$; Fig. 1). For incubating females, neither intercepts nor the slopes of lines relating lipid-reserve dynamics to day of incubation differed significantly between females from Alaska and Manitoba (intercept, $F = 0.26$, df = 1 and 50, $P = 0.61$; slope, $F = 0.16$, df = 1 and 50, $P = 0.61$; Fig. 2).

Discussion

Methodological issues of comparative analysis.—A primary goal of this study was to directly compare patterns of nutrient-reserve use during egg production and incubation by female Northern Shovelers in Alaska and Manitoba. If a sampling correlation exists between stage of reproduction and date of collection, and early nesting females have larger lipid reserves, the failure to include date in the analyses could make it appear that S-lipid is being used for reproduction when it was not. When we included standardized date of RFG in analyses of Manitoba birds, date did not explain significant variation in S-lipid, and S-lipid was still used at a significant rate during egg production. In contrast, S-lipid of Alaska females declined for every day of delay in nest initiation, but females did not use S-lipid to produce eggs. Including standardized date of nest initiation also was important in our S-protein model, because Alaska birds stored protein for each day delay in nest initiation. Interpretation of temporal patterns of nutrient-reserve use for collected birds is difficult because such patterns could be explained by use or storage of a nutrient during egg production, or because females initiating nests later do so with fewer lipid or protein reserves. Regarding lipid models, we favor the second hypothesis for our data because females did not deplete lipid during egg production.

Including date of nest initiation in nutrient-reserve analyses has not resulted in a consistent pattern among species. Date did not explain significant variation in lipid or protein reserves for Gadwalls (*Anas strepera*) during egg production (Ankney and Alisauskas 1991), but it did for Northern Pintails nesting in subarctic Alaska (Esler and Grand 1994). Date explained variation in protein (but not lipid) reserves for pre-RFG and prelaying female Ring-necked Ducks (*Aythya collaris*; Alisauskas et al. 1990). Our analysis of Alaska and Manitoba shovelers shows that the effect of date on nutrient reserves may be site specific and must be evaluated on a study-by-study basis. Certainly, date was an important factor in egg production in Alaska because when we omitted date from our

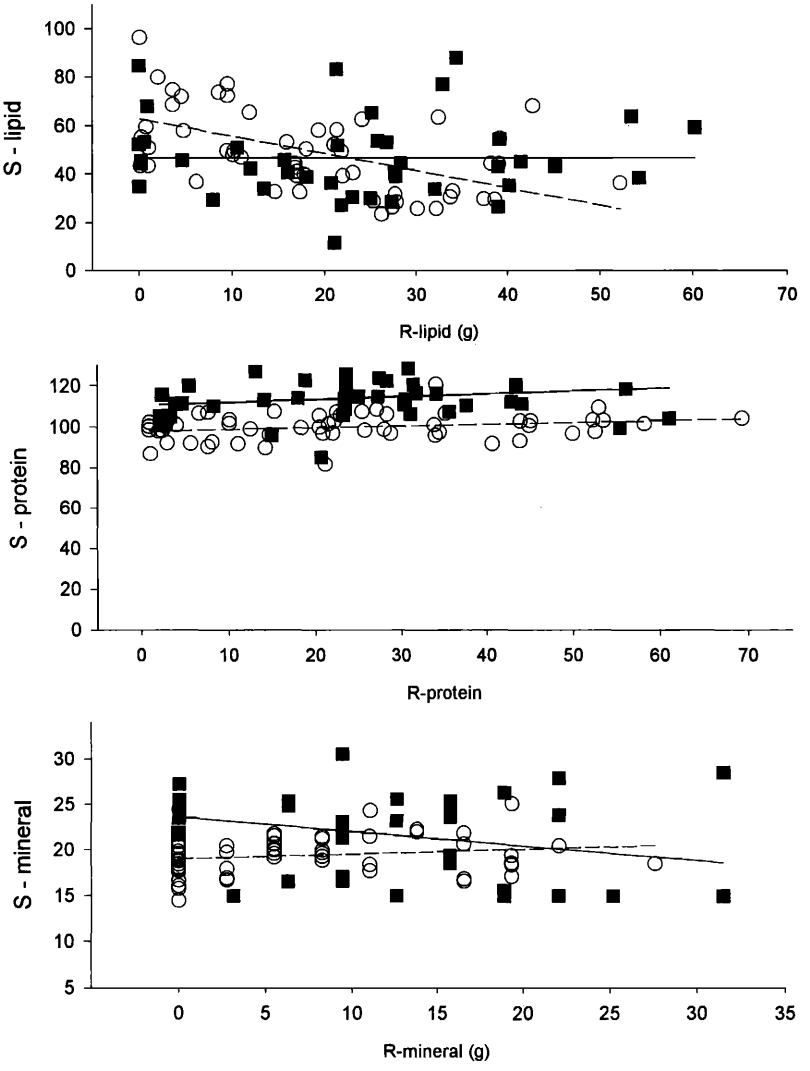

FIG. 1. Commitment of somatic nutrients (protein, lipid and mineral) during egg production for Northern Shovelers in Alaska (closed squares, solid lines) and Manitoba (open circles, dashed lines). Equations for Alaska: S-lipid = 49.27 − 0.02(R-lipid) − 0.76(standardized nest initiation date) + 1.83(body size); S-protein = 108.84 + 0.13(R-protein) + 0.42(standardized nest initiation date) − 0.46(body size); S-mineral = 24.88 − 0.30(R-mineral) − 0.11(standardized nest initiation date) + 1.56(body size). Equations for Manitoba (Ankney and Afton 1988): S-lipid = 63.0 − 0.72(R-lipid); S-protein = 98.3 + 0.07(R-protein) + 3.22(body size); S-mineral = 19.10 + 0.04(R-mineral) + 0.72(body size).

analyses and ran the lipid and protein models as S-nutrient = R-nutrient + body size, the r^2-values were greatly reduced (r^2 = 0.00 and 0.05, respectively), and the models did not explain a significant amount of variation in S-lipid or protein (P = 0.00 and 0.37, respectively).

One explanation for why nutrient-reserve dynamics in Alaska differed from that in Manitoba is that macroinvertebrate abundance in Big Minto Lake (the central area of collection) is comparable to that of temperate lentic systems (Jacobs 1992). Moreover, from 20 May to 20 July, interior Alaska experiences more than 22 h of daylight, and the remaining hours are civil twilight. Therefore, relatively high rates of secondary productivity, coupled with long days, could enable female shovelers to ingest greater quantities of nutrients daily, thereby al-

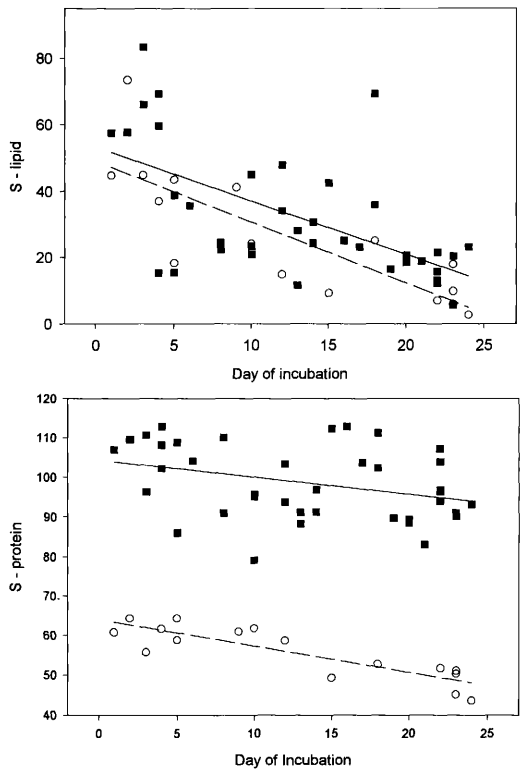

FIG. 2. Decline of somatic lipid and protein during incubation by Northern Shovelers in Alaska (squares, solid line) and Manitoba (circles, dashed line). The S-lipid equations are: S-lipid = 50.55 − 0.98(stage of incubation) − 0.86(standardized nest initiation date) for Alaska and S-lipid = 49.10 − 1.83(day of incubation) for Manitoba. The S-protein equations are: S-protein = 102.6 − 0.41(standardized nest initiation date) − 0.06(stage of incubation) for Alaska and S-lipid = 63.8 − 0.66(day of incubation; Ankney and Afton 1988) for Manitoba. Note that values for Alaska are whole-body protein and those for Manitoba are breast-muscle protein only.

lowing them to maintain energy and protein balance during egg production.

Incubation.—Regression models for lipid dynamics during laying and incubation predicted similar S-lipid at the beginning of incubation (49 and 50.5 g, respectively), indicating that these models were consistent with each other. Incubating shovelers in Alaska used lipid at comparable rates to those in Manitoba (Fig. 2), despite starting with 8% more lipid and spending 11.8% less time on the nest than females in Manitoba (MacCluskie and Sedinger 1999). We do not have behavioral observations from Alaska of female shovelers on incubation breaks, so we cannot determine whether females spend more time off nests because they are in negative energy balance, or because they experience favorable ambient temperatures.

Egg production and regulation of clutch size.—Neither protein nor lipid reserves declined as laying progressed in shovelers nesting in Alaska, in marked contrast with several prairie-nesting duck species that use lipid reserves heavily during egg production (see Alisauskas and Ankney 1992; but see Tome 1984, Dobush 1986, Mann and Sedinger 1993). Our results showing neither storage nor use of any nutrient during egg production also differ markedly from female shovelers in Manitoba. Ankney and Afton (1988) reported that females stored protein at a rate of 0.10 g of S-protein for each gram of R-protein devoted to egg production and depleted lipid reserves at a rate of 0.72 g of S-lipid for each gram of R-lipid. Because use of an endogenous nutrient during egg production is a necessary condition for regulation of clutch size by that nutrient (Sedinger et al. 1997), our data are inconsistent with the hypothesis that clutch size was regulated by nutrient availability to shovelers nesting in interior Alaska.

We observed a pattern of declining lipid reserves with nest initiation date, which is consistent with the hypothesis of individual optimization of reproductive effort (Drent and Daan 1980, Daan et al. 1990). Females that nest later may need fewer reserves to complete breeding because of increased food availability. Ducklings produced by late-nesting females may, however, experience reduced food availability because they hatch after the peak in invertebrate abundance. Thus, the potential cost to females of delaying is reduced duckling survival and a corresponding reduction in recruitment of offspring (Rohwer 1992, Dzus and Clark 1998). In contrast, females that have acquired reserves earlier can nest earlier, thereby increasing survival and recruitment of their ducklings relative to females that nest later (Sedinger et al. 1995).

After controlling for nutrients invested in reproduction, we found no relationships between clutch size and somatic nutrients among females late in laying. This lack of relationship is not consistent with a hypothesis of proximate limitation of clutch size by nutrient availability (Sedinger et al. 1997). Our data therefore indicate that fundamental differences in nutrient

balance during laying occur between females nesting in Alaska versus Manitoba. Studies of shovelers in Alaska and Manitoba suggest a mixed model of clutch size regulation such that when adequate exogenous nutrients are available to females during egg production, clutch size is not limited by nutrient availability and must, therefore, be regulated by ultimate factors. In contrast, when exogenous nutrients are insufficient to meet female requirements during egg production, the ability to supplement nutrient intake from endogenous reserves may limit clutch size.

Most studies that have examined control of clutch size in ducks focused on proximate mechanisms acting on females during egg production. Our data complement two other studies (Tome 1984, Dobush 1986) in providing evidence that in at least some populations, clutch size of most females is not limited by nutrient availability, and some ultimate regulation of clutch size must therefore occur. Future studies should be specifically designed to test for evidence of ultimate regulation of clutch size in ducks while simultaneously considering the energetics of incubation (Ankney et al. 1991).

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