PATTERNS OF NUTRIENT AND ENERGY EXPENDITURE IN FEMALE COMMON EIDERS NESTING IN THE HIGH ARCTIC

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ABSTRACT.—In 1982 we studied weight loss, changes in body composition, and energy expenditure in breeding female Common Eiders (Somateria mollissima borealis) in Svalbard, Norway. Feeding ceased during laying and incubation. From prelaying to hatching, total weight declined by 46.4%, lipid by 81.4%, and protein by 36.8%. Daily energy expenditure during laying was 2,528 kJ, 5.2 times greater than during incubation. Rate of lipid expenditure during laying was 3.3 times greater than during incubation, and rate of protein expenditure was 8.8 times greater. Of the birds' total prelaying energy, 33.8% was expended during laying, 34.6% during incubation, and 31.6% remained at hatching. An estimated 31.6% of the energy expended during laying was invested in eggs. Sixteen- and 18-carbon fatty acids dominated in lipid of the fattest and leanest birds. The major nutrient and energy donors during breeding were 16:0 and 18:1 fatty acids. Svalbard eider eggs weighed ca. 17.5% less and were incubated ca. 1.5 days shorter than eggs from the species' most southerly range limit. This apparent adaptation to arctic existence gave an estimated energy savings of 6.5% during breeding. Received 27 September 1989, accepted 4 April 1990.

DURING reproduction, female waterfowl require substantial nutrients, mainly lipids and protein, both for egg synthesis and as an energy source during laying and incubation. The pattern of nutrient acquisition for and allocation to reproduction differs among various waterfowl species. Some, like the Ruddy Duck (Oxyura jamaicensis), depend almost exclusively on dietary intake throughout breeding (Tome 1984). Ring-necked Ducks (Aythya collaris; Hohman 1986) and Mallards (Anas platyrhynchos; Krapu 1981) obtain most of the protein required for egg production from the diet, while endogenous lipid reserves supply much of the fat needed for egg production and the energy for incubation. Most Arctic-nesting geese, however, feed sparsely during laying and incubation, and draw heavily on endogenous reserves stored before arrival on the breeding grounds (Ryder 1970, Ankney 1977, Ankney and MacInnes 1978, Raveling 1979).

Female Common Eiders (Somateria mollissima borealis) (hereafter, Eiders) feed heavily near nesting islands during the 4–6 weeks before laying, and increase body weight by approximately 20% above winter levels (Gorman and Milne 1971). They then fast completely during incubation (Cooch 1965: 30, Gorman and Milne 1971, Milne 1976, Korschgen 1977) and apparently during laying as well (Korschgen 1977); the nutrients and energy required for both producing and incubating a clutch of eggs are drawn entirely from endogenous reserves. The Eider represents an extreme case of seasonal negative energy and nutrient balance in breeding birds.

Milne (1976) and Korschgen (1977) investigated changes in the body weight and composition of Eiders throughout the year, and Korschgen (1977) studied weight changes in selected organs and muscles mainly during incubation. Neither study presented detailed data on the changes in weight and body composition that occur in laying when the rate of energy and nutrient expenditure is substantial. Our aim was to investigate the extent and pattern of endogenous nutrient and energy expenditure during laying and incubation in female Eiders breeding in the high Arctic. We also provide comparative data from a population breeding near the species' northern range limit.

STUDY AREA AND METHODS

The study was conducted at Ny-Ålesund in the Kongsfjord region of West Spitsbergen (78°55′N,

12°00′E) in the Svalbard (Norway) archipelago during 1982. Eiders returned to the Kongsfjord region around mid-April after wintering farther south. Birds concentrated in patches of open water near the mouth of the fjord to forage before nesting. Pairs began flights to the inner fjord in late May, apparently to investigate ice conditions near breeding islands there. Eiders usually concentrate breeding efforts on five major islands in the inner Kongsfjord, as well as near the research station at Ny-Ålesund. Laying often begins at different times on adjacent islands because of local variation in ice conditions (Parker and Mehlum in press). Consequently, all birds collected for body composition analysis were collected at the Ny-Ålesund colony. Females were collected at four precisely known stages of the reproductive cycle designated as (1) *two-three weeks before laying*: females collected shortly after pairs began to arrive near the Ny-Ålesund colony (i.e. 2–3 weeks before laying began [$n = 4$]); (2) *prelaying*: females with large follicles collected just before laying and within 3 days of commencement of laying in the colony ($n = 7$); (3) *postlaying*: females collected after 2–3 days of incubation (mean $= 2.1$), each checked regularly during laying to minimize the possibility of dump nesting or loss of eggs to predators ($n = 7$); and (4) *hatching*: females collected on the nest with hatched or hatching young ($n = 8$). An additional 14 females at this stage were captured and weighed to increase the sample size of bird weights at hatching.

Immediately after collection, birds were weighed (total carcass weight) on a Salter spring scale to the nearest 10 g. They were then completely hand-plucked and singed. The intestines (emptied), gizzard (emptied), liver, both pectoral muscles, and the ovary with oviduct were excised, and wet weights were recorded to the nearest 0.1 g. The featherless carcass (including excised muscles and organs) was weighed (featherless carcass weight) and frozen at $-20°C$ in double plastic bags.

In preparation for the body composition analysis, the frozen material was sawed on a band saw into pieces and homogenized in a food grinder. The water content of each carcass was determined by drying duplicate 15-g samples to constant weight in a vacuum oven for 2 days at room temperature and ca. 1 day at 30°C. The remaining material was burned at 600°C to constant weight (for approx. 4 h) to obtain ash values. Total lipid was determined with a modified Folch extraction (chloroform-methanol), and total protein by the macro-Kjeldahl method with protein expressed as the product of nitrogen times 6.25. Both lipid and protein determinations were based on 6–10 g samples, usually in triplicate (Holm et al. 1973). Calculation of energy content in lipid is based on a conversion factor of 38.53 kilojoules per gram (kJ·g^{-1}), as direct calorimetry of fat samples ($n = 9$) from both fat and lean birds gave this same value. The energy content of protein was derived using a stan-

dard conversion factor of 19.67 kJ·g^{-1} (Pullar and Webster 1977). The energy in subsamples of total homogenate from nine different carcasses, including individuals from each of the four classes of breeding birds, was determined by direct calorimetry. These direct values were compared with total energy values of the same birds derived by calculation as a check for accuracy. Energy values throughout are expressed in kilojoules (4.184 kJ = 1 kcal). Samples of homogenate from the fattest bird collected 2–3 weeks before laying and the leanest bird collected at hatching were analyzed for fatty-acid composition using standard gas chromatography methods.

All analyses were done at the Institute for Nutrition Research, School of Medicine, University of Oslo, Oslo, Norway. Statistical comparisons of carcass, organ, muscle, lipid, protein, water, and ash weight were made using one-way analysis of variance with significance level set at $P < 0.05$.

RESULTS

Changes in body and organ weight.—The first Eider pairs were seen flying over the nesting islands near the inner fjord on 1 June 1982. On 3–4 June the first 4 females were collected. Total carcass and organ weights of these birds did not vary significantly from those of prelaying birds collected on 16–17 June with the exception of the ovary and oviduct (Table 1). On 3–4 June ovaries had begun to recrudesce and mean ($\pm$SD) diameter of the largest follicle was 13 ± 7 mm (range 7–22 mm, $n = 4$). The ovary and oviduct of prelaying birds collected on 16–17 June were approximately 8 times heavier with a mean diameter of the largest follicle of 40 ± 6 mm (range 32–48, $n = 6$). Presumably these birds had entered the phase of rapid follicular development and were about to lay. The difference (120 g) in mean total carcass weight between these two groups was identical to the mean weight increase in the ovary and oviduct between the two periods.

A major and significant change occurred in total carcass weight and all muscle and organ weights between the prelaying and postlaying groups. Total carcass weight declined 30.6%, the pectorals 17.2%, gizzard 35.5%, liver 62.7%, intestines 42.5%, and ovary plus oviduct 88.6%. Regression of the ovary during this period amounted to 15.6% of the total weight loss. Females lost 22.8% of their carcass weight between postlaying and hatching, and there was a significant decline in the weight of all organs and muscles during incubation. Total carcass weight between prelaying and hatching declined 46.4%,

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TABLE 1.   Changes ($\bar{x} \pm$ SE) in wet weight (g) of the total carcass, both pectoral muscles, gizzard, liver, both intestines, and ovary plus oviduct in female Common Eiders in Svalbard.

Stage	Carcass	Pectorals	Gizzard	Liver	Intestines	Ovary + oviduct
			Breeders			
2–3 weeks before						
laying	2,433 ± 127	400.1 ± 17.6	57.0 ± 4.9	77.2 ± 2.3	71.0 ± 3.6	17.1 ± 5.2
range	2,230–2,800	369.8–450.8	44.4–67.2	72.0–82.7	62.1–79.6	4.7–27.1
n	(4)	(4)	(4)	(4)	(4)	(4)
P^a	NS	NS	NS	NS	NS	**
Prelaying	2,553 ± 83	406.9 ± 14.9	48.6 ± 4.9	84.9 ± 7.5	64.1 ± 4.8	137.1 ± 24.0
range	2,310–2,880	361.5–458.2	29.2–70.7	52.3–116.2	41.6–80.7	69.2–212.9
n	(7)	(7)	(7)	(7)	(7)	(6)
P	***	**	**	***	***	***
Postlaying	1,773 ± 62	337.0 ± 11.5	31.2 ± 2.0	31.7 ± 2.0	36.9 ± 3.3	15.7 ± 1.1
range	1,470–1,940	297.6–384.9	24.3–39.0	27.1–40.0	27.0–53.1	11.8–21.3
n	(7)	(7)	(7)	(7)	(7)	(7)
P	***	***	***	**	***	***
Hatching	1,368 ± 25	279.1 ± 7.1	21.4 ± 1.1	22.6 ± 1.1	23.0 ± 1.2	3.0 ± 0.2
range	1,210–1,640	248.2–307.1	17.1–26.3	20.0–27.4	18.2–27.7	2.0–4.0
n	(22)	(8)	(8)	(8)	(8)	(8)
			Nonbreeders			
Prelaying[b]	2,025 ± 5	352.7 ± 12.9	75.1 ± 8.6	89.1 ± 3.1	106.8 ± 5.5	2.5 ± 0.1
range	2,020–2,030	339.8–365.6	66.5–83.7	86.0–92.2	101.3–112.3	2.4–2.6
n	(2)	(2)	(2)	(2)	(2)	(2)

[a] P = probability (from one-way ANOVA) that adjacent means within a column are significantly different. ** = $P < 0.01$; *** = $P < 0.001$; NS indicates no significant difference ($P > 0.05$).

[b] Nonbreeding females collected simultaneously with prelaying breeders.

the pectorals 31.4%, gizzard 56.0%, liver 73.4%, and intestines 64.2%.

We observed that females did not eat during laying or incubation. The wet weight of intestinal contents supported this. The guts of birds collected 2–3 weeks before laying contained on average 34 g, 25 g at prelaying, 9 g at postlaying, and 0 g at hatching.

Two females collected with the sample of prelaying birds proved to be nonbreeders, as indicated by their dormant ovaries. Both were accompanied by males when collected and were impossible to separate from breeding females before collection. Despite this small sample, there were some obvious differences between nonbreeders and breeders, which may help to elucidate the pattern of nutrient storage and mobilization. Total carcass weight of nonbreeders averaged 20.7% below that of prelaying breeders, and the pectorals averaged 13.3% below. The gizzard was 54.5% greater in nonbreeders, and the intestines 66.4% greater.

Changes in body composition.—The mean energy content in subsamples from nine featherless carcasses derived from direct calorimetry did not differ significantly (t-test, $P > 0.05$) from the mean value calculated using standard body

composition conversion factors. Calculated values were therefore considered sufficiently accurate.

Neither featherless carcass weight nor weight of lipid, protein, water, or ash changed significantly from 2–3 weeks before laying to prelaying (Table 2). We suggest that the first breeding birds to arrive near the breeding grounds had already attained maximum body condition. During the 6–7 days between prelaying and postlaying, all weights declined significantly: featherless carcass weight by 31.1%, lipid 41.0%, protein 27.2%, and ash 23.0%. This shows a rapid rate of endogenous nutrient mobilization. The relative proportion of the 4 body components changed little. Weight loss continued to decline significantly from postlaying to hatching, with the exception of ash. Remaining lipid declined 68.4% during incubation, and only 9.6% of the body was lipid at hatching. Protein, in contrast, declined by only 14.3%. During the entire period from prelaying to hatching, lipid weight declined 81.4% and protein 36.8%. Protein loss between pre- and postlaying was 112.7 g (16.8 $g \cdot day^{-1}$), but only 43.0 g (1.9 $g \cdot day^{-1}$) from postlaying to hatching, which implies that protein reserves were being expended mainly during

TABLE 2. Changes ($\bar{x} \pm$ SE) in weight (g) of whole featherless carcass, lipid, protein, water, and ash of female Common Eiders in Svalbard.

Stage	Carcass	Lipid	Protein	Water	Ash
Breeders					
2–3 weeks before					
laying	2,270 ± 114	645.8 ± 73.5	386.8 ± 9.7	1,136.4 ± 33.6	74.6 ± 1.5
% of total	—	28.5	17.0	50.1	3.3
range	2,070–2,590	471.6–821.8	371.2–413.9	1,073.5–1,229.5	72.2–78.5
n	(4)	(4)	(4)	(4)	(4)
P^a	NS	NS	NS	NS	NS
Prelaying	2,407 ± 81	638.5 ± 34.0	413.9 ± 16.7	1,232.4 ± 45.3	80.3 ± 3.3
% of total	—	26.5	17.2	51.2	3.3
range	2,180–2,740	462.2–748.6	350.6–476.2	1,030.5–1,363.2	69.5–92.6
n	(7)	(7)	(7)	(7)	(7)
P	***	***	***	***	***
Postlaying	1,659 ± 58	377.0 ± 27.8	301.2 ± 7.4	892.0 ± 24.9	61.8 ± 2.6
% of total	—	22.7	18.2	53.8	3.7
range	1,370–1,810	260.3–470.2	264.0–323.8	773.5–969.1	53.7–70.8
n	(7)	(7)	(7)	(7)	(7)
P	***	***	**	**	NS
Hatching	1,238 ± 32	119.0 ± 18.9	258.2 ± 5.2	779.4 ± 20.8	59.4 ± 2.1
% of total	—	9.6	20.9	63.0	4.8
range	1,120–1,410	55.2–218.9	239.0–283.3	699.4–874.5	52.3–68.8
n	(8)	(8)	(8)	(8)	(8)
Nonbreeders					
Prelaying[b]	1,905 ± 5	240.5 ± 49.2	368.0 ± 4.7	1,187.4 ± 36.4	77.7 ± 8.0
% of total	—	12.6	19.3	62.3	4.1
range	1,900–1,910	191.3–289.7	363.3–372.6	1,151.0–1,223.8	69.7–85.7
n	(2)	(2)	(2)	(2)	(2)

[a] P = probability (from one-way ANOVA) that adjacent means within a column are significantly different. ** = $P < 0.01$; *** = $P < 0.001$; NS indicates no significant difference ($P > 0.05$).

[b] Nonbreeding females collected simultaneously with prelaying breeders.

egg production. The proportion of water in the body increased from 51.2% at prelaying to 63.0% at hatching. The 2 nonbreeding females collected simultaneously at prelaying contained 62.3% less lipid and 9.9% less protein than breeders.

Energy expenditure during laying and incubation.—We calculated that, based on weight loss of lipid and protein (Table 2), birds used on average 12,656 kJ during laying and the first 2.1 days of incubation. Average energy expended during incubation was 490 kJ·day⁻¹ (see below). Eiders lay at a rate of 1 egg per day (Hagelund and Norderhaug 1975), and the mean clutch size of the 7 birds in the sample of postlayers was 4.6 (range 4–6). Subtracting the energy expended during 2.1 days of incubation (i.e. 1,029 kJ) from 12,656 kJ gives 11,627 kJ (78.5% from lipid) expended during the average 4.6-day laying period, or a daily energy expenditure (DEE) during laying of 2,528 kJ. Average egg weight after a mean of 2.1 days of incubation was 104 g, or 478 g of fresh eggs in the

average clutch. Korschgen (1977) found that fresh Eider eggs ($\bar{x} = 126$ g) contained on average 15 g of protein and 17.5 g of lipid. Using energy values of 38.53 kJ·g⁻¹ for lipid and 19.67 kJ·g⁻¹ for protein, we arrived at a value of 7.69 kJ·g⁻¹ of fresh egg weight. This is close to Ricklef's (1974: 182) value of approximately 7.32 kJ·g⁻¹ for waterfowl eggs. Thus a mean clutch of 4.6 eggs contained 3,677 kJ, or 31.6% of the energy expended during laying.

During our study 30 females in the Kongsfjord area that were kept under close scrutiny used an average (±SD) of 24.2 ± 0.8 days (range 22–26) from the day the last egg was laid until hatching. Assuming a 24.2-day incubation period, the time span from postlaying to hatching was 24.2 minus 2.1 (22.1) days. Mean energy expenditure for birds during this period was 10,832 kJ (91.8% from lipid) or a DEE during incubation of 490 kJ. The DEE during laying was 5.2 times incubation DEE. Of the total energy contained in birds just before laying, 33.8% was expended during 4.6 days of laying, 34.6%
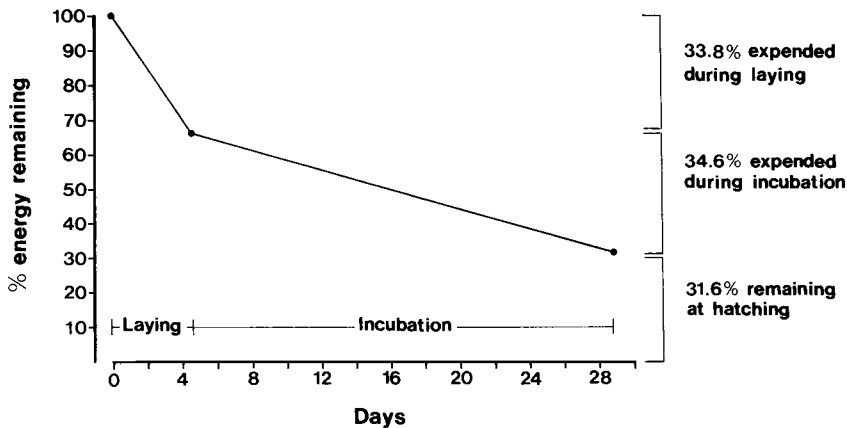
Fig. 1. Proportion of prelaying energy in body reserves expended by female Common Eiders during laying and incubation, and that which remained at hatching.

was expended during 24.2 days of incubation, and 31.6% remained at hatching (Fig. 1).

Changes in fatty acid composition.—Fatty acid composition of the fattest female (31.7% lipid) collected 2–3 weeks before laying was compared with that of the leanest female (4.5% lipid) collected at hatching (Fig. 2). The dominant fatty acids in the fat bird were 18:1 (34.6%) and 16:0 (27.4%), with lesser proportions of 16:1 (12.1%) and 18:0 (7.3%). Predominant fatty acids in the lean bird were 18:1 (40.5%) and 16:1 (21.7%), while 16:0 declined to 1.4%. Changes in the proportion of other fatty acids were minor. Mean lipid loss from prelaying to hatching was 520 g, of which an estimated 76% was due to the combined catabolism of 18:1 (33%), 16:0 (33%), and 16:1 (10%).

DISCUSSION

The first females to arrive near breeding islands had apparently attained maximum body condition (Table 2). These individuals seemed to make daily flights between feeding areas near the outer fjord and breeding islands farther into the fjord. In this manner body condition could be maintained until laying, while birds monitored ice conditions near breeding islands. In years of late ice breakup (e.g. 1982), it was probably important for pairs to keep close watch on breeding islands to compete for the best nesting sites when breakup finally occurred.

Weight loss during laying and incubation.—Female Eiders increase body weight ca. 20% during the 4–6 weeks before laying (Gorman and

Milne 1971, Milne 1976, Korschgen 1977). Korschgen's (1977) limited data (1 prelaying bird) suggested that weight gained before laying was about equal to that lost during laying. We found that total carcass weight declined by 29% (19% of which was clutch weight) during the 4.6-day laying period. If we assume that arctic Eiders also increase body weight ca. 20% before laying (2 prelaying nonbreeders, at least, were 21% lighter than prelaying breeders), then weight loss during laying was slightly greater than the prelaying weight gain. Thus, the prime function of this weight gain appears to be the storage of nutrients and energy necessary for egg production.

The rapid weight loss of the pectorals, gizzard, liver, and intestines during laying suggests that each contributes nutrients to egg synthesis. Storage of protein and fat appears to occur in Eiders before laying, as reported for Red-billed Quelea (*Quelea quelea*; Kendall et al. 1973, Jones and Ward 1976), Lesser Snow Geese (*Chen c. caerulescens*; Ankney and MacInnes 1978), and Canada Geese (*Branta canadensis minima*; Raveling 1979). Korschgen (1977) found that the pectorals of wintering Eider females averaged 290 g, and that one female had pectorals weighing 397 g just before laying. We do not have data on winter pectoral weights, but in 7 prelaying females, the pectorals averaged 407 g. Postlaying weight of pectorals averaged 337 g, similar to the 340 g found by Korschgen (1977; *n* = 12). Thus, the combined data suggest that pectoral weight increases by approx. 110 g (38%) between winter and prelaying, and declines by
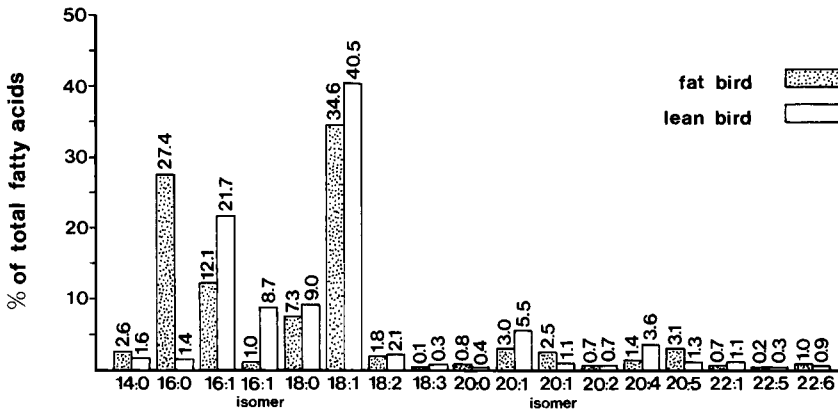
Fig. 2.   Fatty-acid composition of total extractable lipid in the fattest female Common Eider collected 2–3 weeks before laying (31.7% lipid), and the leanest collected at hatching (4.5% lipid). Percentages are indicated above columns.

approx. 60 g during laying. How much of this increase is due specifically to changes in protein is unknown. Milne (1976) also suggested that female Eiders store protein before laying.

Considerable protein may also be stored in the gizzard before laying. Korschgen (1977) recorded an 83% weight loss in the gizzard from the early stages of follicle development to the start of incubation. In nonbreeders (collected simultaneously with prelaying breeders), we found gizzards that were 32% heavier than breeders 2–3 weeks before laying. We believe that a considerable loss occurred from the gizzard in breeders during the early follicle development period. Korschgen (1977) estimated that protein loss from the gizzard alone during egg formation was sufficient to provide 38% of the protein required for clutch formation. The emptied intestines of prelaying nonbreeders were also considerably heavier (50%) than breeders 2–3 weeks before laying. We do not know how much of the early weight loss from the gizzard and intestines is due to simple atrophy following hyperphagia, or to a possible change in diet, and how much is due to nutrient mobilization connected with follicle development. We found that liver weight declined by 63% and the intestines by 43% during the 4.6-day laying period, which indicates the extreme mobility of nutrients in these organs during combined fasting and reproduction.

The pectorals maintained full weight before laying. During both laying and incubation, they lost comparatively less than both the whole body and the other organs measured. With the di-

gestive tract at a low activity level, the heat generated by the pectorals becomes even more important as a source for incubation. They also provide the main means of escape from predators. These two factors may help to explain the greater weight loss from other organs during this period.

Milne (1976) reported that female Eiders became dehydrated during laying and early incubation, and attributed this to the water demands of egg production. We found that absolute water loss was significant between pre- and postlaying, though relative water content did not change. Presumably birds did not become dehydrated during laying.

During incubation, total carcass weight declined by an additional 25% (adjusted for the entire 24.2-day incubation period). Likewise, all organ weights decreased, which implies that each functioned as an energy supplier during this period. Slightly greater incubation weight losses were recorded in Eiders (33%, Korschgen 1977; 28%, Hario 1983; 36%, Kuresoo and Paakspuu 1983; and 36%, Gabrielsen et al. in press).

Females lost an average of 112.7 g of protein during laying and the first 2.1 days of incubation, though only 57.0 g (50.6%) was estimated to have been deposited in the clutch. Raveling (1979) found that both male and female Canada Geese experienced significant protein loss from, among other sites, the liver and gizzard during their mates' laying periods. This supports our observation that considerable protein was expended for purposes other than egg production. Lipid loss during this same period averaged

261.5 g, of which only 66.2 g (25.3%) was esti-
mated to have been deposited in the clutch.
Arctic-nesting Canada Geese, which feed very
little during laying, deposited a similar pro-
portion (17.2%) of the fat lost during laying in
eggs (Raveling 1979).

Changes in fatty acid composition.—Sixteen- and
18-carbon fatty acids dominated in the total ex-
tractable body fat of both the fattest and leanest
females, and apparently are the dominant fatty
acids in all birds tested thus far (Blem 1976).
Johnson and West (1973) found that 18:1 and
16:0 were dominant fatty acids in Adélie Pen-
guins (*Pygoscelis adeliae*), which like Eiders are
anorectic during breeding. In birds, 16:0 fatty
acid is highly labile and can be an important
nutrient and energy supplier during both lay-
ing and incubation.

*Ecological significance of anorexia in female Ei-
ders.*—Breeding anorexia probably occurs in Ei-
ders primarily as a defense against gulls and
other avian egg predators (Bourget 1973, Camp-
bell 1975, Choate 1967, Milne and Reed 1974,
Korschgen 1977). We observed that, even though
gulls are common on arctic nesting islands, they
rarely attack a well-guarded Eider nest. How-
ever, we suggest that the Eiders' pattern of nest-
habitat selection may also have influenced the
development of breeding anorexia. Eiders usu-
ally select small islands as nest sites, apparently
for protection from red (*Vulpes fulva*) and arctic
foxes (*Alopex lagopus*), and not primarily for their
proximity to good feeding sites. In Svalbard,
these islands are limited in number and may
be located at considerable distances from areas
with abundant food during the nesting season.
Therefore, even without gulls, the need to feed
during nesting would often entail traveling long
distances each day and thereby increase the
clutch's exposure to precipitation and low am-
bient temperatures. Several species of arctic
geese which nest when food is scarce also be-
come anorectic as part of their reproductive be-
havior (Ryder 1970, Ankney 1977, Raveling
1979).

Body reserves and clutch size.—Arctic-nesting
geese feed little during laying and incubation
(Ryder 1970, Ankney 1977, Raveling 1979), and
they show a pattern of weight and nutrient loss
during breeding similar to the Eiders (Ankney
and MacInnes 1978, Raveling 1979). Ankney and
MacInnes (1978) found that female Lesser Snow
Geese with the largest nutrient reserves pro-

duced the largest potential clutches. This sug-
gested that actual clutch size in this species was
determined by the size of nutrient reserves. The
amount of nutrient reserves expended during
laying by female Eiders is almost equal to the
amount stored just before laying (Milne 1976,
Korschgen 1977). Thus, clutch size in Eiders
predictably is dependent upon the level of body
reserves stored before laying. Milne (1976)
found a positive correlation between winter
body weight of female Eiders and clutch size
the following spring.

Raveling and Lumsden (1977) proposed that
egg laying in arctic geese ceased when body
weight had declined to winter or "basal" levels,
and that reserves above winter levels were al-
lotted mainly to eggs. Proximal control of clutch
size therefore was dependent upon the deple-
tion of some essential body material(s). Results
from Milne (1976), Korschgen (1977), and our
study tend to support this hypothesis for Eiders.

Most Svalbard Eiders winter farther south,
probably from mid- to northern Norway, as well
as near Iceland (Nils Røv pers. comm.). Pairs
returned to the Kongsfjord region from mid-
April to early May. In normal-ice years, most
nests are initiated during the first 2 weeks of
June. Therefore, the accumulation of prelaying
reserves probably occurs at Svalbard and not on
wintering areas. Spring breakup along coastal
Svalbard (where Eiders feed before laying)
shows considerable annual variation (Parker and
Mehlum in press). Thus prelaying nutrient stor-
age—and consequently clutch size—in Sval-
bard Eiders may be influenced by ice condi-
tions.

Late spring breakup delays both access to
nesting islands and nest initiation in arctic Ei-
ders during some years (Lack 1933, Ahlèn and
Anderson 1970, Quinlan and Lehnhausen 1982,
Parker and Mehlum in press). Delayed nesting
in turn results in reduced clutch size in arctic
nesting geese and Eiders (Barry 1962; Ryder
1967, 1972; Ahlèn and Anderson 1970; Raveling
and Lumsden 1977). Body reserves probably be-
gin to decline while birds wait for nesting sites
to become available. Female Eiders, however,
may tolerate a certain degree of nesting delay
before stored reserves begin to decline, as there
was no significant difference in body weight or
reserve levels between females collected near
nesting sites 2–3 weeks before laying and just
before laying. Thus, prelaying body condition

may be maintained for several weeks by commuting between feeding and nesting sites while waiting for nesting islands to become available.

Arctic versus southern populations.–The Kongsfjord Eider population at 79°N latitude nests near the species' northern range limit. In North America (Korschgen 1977), the species' southern breeding limit is at 44°N latitude. Despite a 35° difference in breeding-site location, the pattern of nutrient and weight change during breeding appears to be essentially the same.

Some differences exist. We found that 32 Eider eggs incubated only 2–3 days had a mean weight of 104.0 g. Likewise, Hagelund and Norderhaug (1975) found that 33 fresh Eider eggs from another Svalbard nesting site averaged 104.8 g (range = 94–117 g). Korschgen (1977), however, cited 126 g as the average fresh weight of Eider eggs in Maine (no sample size given). At Svalbard, 30 females incubated for an average of 24.2 days (range 22–26), whereas Hagelund and Norderhaug (1975) measured mean incubation times of 24.3 days for 410 Svalbard nests in 1969, and 24.8 days for 68 nests in 1970. Eastern North American Eiders, in contrast, incubate for 26 days (Guignion 1968, Korschgen 1977). Mean clutch size in our study (first clutches) was 4.6, which is identical to Sarbello's (1973: 34) value for 14 first clutches of Maine birds. We assumed a 24.5-day incubation period and mean egg weight of 104 g for the Svalbard population, a 26-day incubation period and mean egg weight of 126 g for the Maine population, and equal clutch size. It was possible to calculate some of the energy savings involved in laying eggs that were 22 g lighter and incubated 1.5 days fewer. If we assume a clutch size of 4.6, reduction of fresh egg weight by 17.5% would save 778 kJ in egg material, or 6.7% of the total energy expenditure during the 4.6 days of laying. Smaller eggs should also require less energy to produce and incubate. Shortening the incubation period from 26 to 24.5 days (5.8%) would save 735 kJ. Total energy savings for laying and incubation combined would be 6.5%, which presumably reflects an adjustment to high arctic conditions.

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