THE ENERGETICS OF MIGRATION AND REPRODUCTION OF DUSKY CANADA GEESE[1]

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Abstract. We analyzed the carcass composition of 160 adult female Dusky Canada Geese (*Branta canadensis occidentalis*) collected in Oregon and Alaska from 1977 to 1979, to determine energy use patterns from premigration to hatch. We tested the predictions that geese would accumulate energy reserves during migration, experience a gradual loss during prelaying and a severe loss during laying and incubation. Energy requirements met from food were estimated by comparing changes in endogenous reserves to estimated daily energy requirements. Body mass, and water, lipid and protein components varied by stage of reproduction ($P = 0.0001$), and protein also varied by year ($P = 0.0001$). The brief migration period was costly, with a 52% decline in lipids, indicating that strategies to meet these energy demands are pivotal and will influence subsequent energy dynamics of reproduction. Geese maintained or increased lipid and protein reserves during the prelaying period, gradually lost reserves during laying and experienced considerable declines during incubation. Use of food for energy and nutrient requirements was important at all stages, accounting for 24% during incubation, the smallest but perhaps most critical contribution, to 100% during prelaying, of estimate daily energy requirements. The contribution of exogenous (food), versus endogenous sources, to energy and nutrient requirements of northern nesting geese is proving to be much more important than previously thought.

Key words: *Dusky Canada Goose;* Branta canadensis occidentalis; *energetics; migration; reproduction.*

INTRODUCTION

The role of exogenous versus endogenous reserves during migration and reproduction in geese is poorly understood. Most species apparently increase lipid and protein components during migration (Hanson 1962, Ryder 1967, Raveling 1979a, Wypkema and Ankney 1979, Thomas 1983) but some acquire reserves on wintering grounds (McLandress and Raveling 1981, Vangilder et al. 1986). On the nesting grounds, arctic geese have been regarded as independent of food during the prelaying period (Ryder 1970, Ankney and MacInnes 1978, Raveling and Lumsden 1977). Consequently several researchers have postulated a direct relationship between clutch size and amount of endogenous reserves (Ryder 1970, MacInnes et al. 1974, Newton 1977, Ankney and MacInnes 1978). This conclusion was a modification of Lack's (1967) proposal that clutch size of waterfowl evolved in relation to the average availability of food for females at the time

of laying. Consequently, emphasis shifted from a belief in reliance upon food in the first case, to essentially total dependence upon reserves in the second case.

Laying and incubating females apparently are under considerable stress as evidenced by minimal body mass and occasionally even death by starvation during late incubation in geese and eiders (Harvey 1971, Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979a). Periods of the reproductive season are interdependent (Ricklefs 1974), and the role of food versus endogenous reserves must have considerable implications in the evolution of strategies to meet the energy demands of migration and reproduction in northern nesting geese (see Drent and Daan (1980) for a general discussion relative to all birds). Brant (*Branta bernicla bernicla*) have been found to use food extensively during laying and incubation (Ankney 1984) and female Greater White-fronted Geese (*Anser albifrons frontalis*) and Greater Snow Geese (*Chen caerulescens atlantica*) maintain or increase reserves during prelaying on breeding grounds (Budeau et al. 1991, Choiniere and Gauthier 1992).
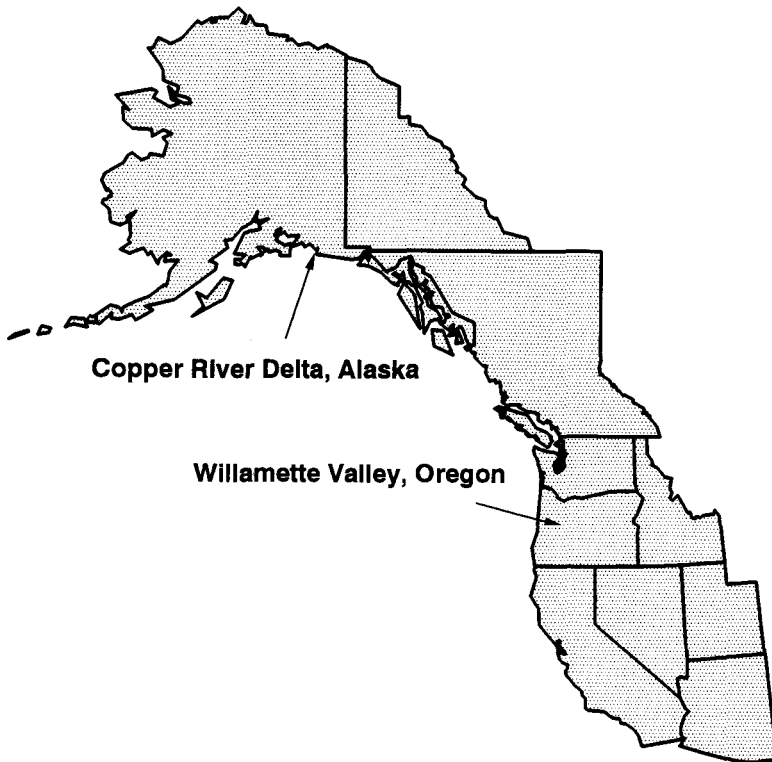
FIGURE 1. Study area locations on the wintering grounds in Oregon, and breeding grounds in Alaska, of Dusky Canada Geese.

We wished to test the hypotheses that (i) exogenous sources of lipid and protein are not important to geese during reproduction, and (ii) that variation in endogenous reserves during different stages simply reflects demands during those periods. Based on the work of Barry (1967), Ryder (1970) and Raveling and Lumsden (1977), which suggested that geese arrive on nesting grounds at peak condition, we predicted that geese would build reserves during premigration and migration, arrive at peak body condition for the season, and that reserves would gradually decline during prelaying, and steeply decline during laying and incubation. To address these questions, we examined the energetics of migration and reproduction in female Dusky Canada Geese (*B. canadensis occidentalis*) during 1977–1979. Specific objectives were to: (1) determine body mass and the water, protein, and lipid content of adult female geese from premigration to hatching of eggs, (2) determine the net change in lipid and protein reserves among five defined stages of re-

production, and (3) assess the contributions of exogenous and endogenous lipid and protein to estimated daily energy requirements for each reproductive period.

METHODS

STUDY AREA

Geese were collected on the Willamette Valley National Wildlife Refuge (NWR), Oregon and on the Copper River Delta (CRD), Alaska (Fig. 1). The Willamette Valley in western Oregon is dominated by small grain and grass seed agriculture (Highsmith and Kimerling 1979). The three refuges comprising the Willamette Valley NWR and adjacent farmland provided winter habitat for a major proportion of the Dusky Goose population during the study (Simpson and Jarvis 1979, J. C. Cornely, USFWS, unpubl. data). Geese staged on the refuges in late March and early April, with major exodus between 8 and 14 April (Chapman et al. 1969, and pers. obs.) The second

study area was the west side of the CRD in south central Alaska (60°22'N, 145°23'W). Research was concentrated on the area (14 km²) of highest density of goose nests. This area was intersected by a network of tidal sloughs and dotted with ponds up to 6 ha in size. The climate of the area is characterized by long cool winters and short cool summers (USDC 1977–1979). The timing of complete snow melt in spring varies from mid-April to late May, but consistently occurred in mid to late April during the three seasons of this study.

PHENOLOGY AND COLLECTIONS

The date of complete snow melt on the study area was recorded each year. Once the first eggs were found, areas were searched for nests to determine clutch size and initiation of laying dates each year. A sample of nests was monitored to determine apparent nest success. Major arrival dates on breeding grounds were estimated based upon impressions gained during aerial and boat surveys of the study area during mid- to late April each year.

Adult female geese were collected by shooting during daylight hours in 1977, 1978 and 1979. Geese were weighed within 6 hr of collection. In Oregon, specimens were frozen within 2 hr. On the nesting grounds, geese were frozen within 48 hr of collection after storage under cool conditions (≤10°C). Geese were grouped according to stage of reproduction: Premigration (within 12 days of departure from the wintering grounds); Arrival (arrival on the nesting ground; largest ovarian follicle less than 25 mm in diameter); Pre-laying (geese collected just prior to, at or just after initiation with at least one ovarian follicle larger than 25 mm in diameter and no more than one oviposited egg); Mid-laying (geese collected with 40 to 75% of their potential clutch layed, as determined from ruptured and enlarged follicles); Post-laying (all enlarged follicles ovulated; 1st or 2nd day of incubation); Hatch (from within four days of hatching of eggs to one day after hatching). The composition of Mid-laying geese, reported in Appendix 1, was only used in analyses of changes in carcass components with increasing commitments to reproductive tissues, as discussed below. In addition to stages of reproduction, four periods of the "reproductive season" were defined as: Migration period (from premigration stage to arrival; 11 days); Prelaying period (from arrival to pre-lay stage; 11 days);

Laying period (from pre-lay to post-lay; 8 days); Incubation period (from post-lay to hatch; 27 days).

CARCASS COMPOSITION

Feathers were sheared from frozen specimens. The bill and feet were removed and the carcass reweighed. After partial thawing, oesophageal contents were taken from the carcass and preserved for later identification (reported in Bromley 1984). The ovary was excised and examined for ovulated or enlarged follicles. Diameter of the largest follicle was measured to the nearest 0.05 mm; the ovary and oviducal egg (also removed, if present) were then homogenized for analysis of water, lipid and protein content separate from the carcass. The partially frozen carcass was sectioned and homogenized. Body mass refers to the mass of the entire goose at the time of collection. Carcass components, including water, lipid and protein, refer to the mass of the goose after removal of feathers, bill, feet, oesophageal contents and ovary, including oviducal eggs. Unlike studies conducted after these data were collected, we included the oviduct in the carcass analyses rather than in analyses of reproductive tissue. We considered that, while development of the oviduct can be a demand on energy and nutrient reserves, it also becomes an energy and nutrient source available during the incubation period after laying is completed. Water and lipid content were determined for triplicate 30 g samples of homogenate. Water content was assessed by drying samples in a forced air oven at 55°C to constant mass (Ricklefs 1974). Lipid content was determined from the triplicate samples by extraction in a soxhlet apparatus with a 1:1 methanol/chloroform fat solvent for 22 hr. The solvent was replaced once after the first 11 hr. Nitrogen was measured from duplicate 5 g samples using the Kjeldahl method, and converted to crude protein by multiplying by a conversion factor of 6.25 (Horowitz 1970:16, 127).

We examined the relationship between carcass components (lipid and protein) and reproductive lipid and protein of individual pre-lay, mid-lay and post-lay geese, following the methodology of Alisauskas and Ankney (1985:136), with one exception. Reproductive tissue included the lipid and protein components of the ovary, and oviducal and oviposited eggs, but not the oviduct.

Energy reserves were defined as the energy yield from oxidation of lipid and protein not required

for the basic structure of the average living goose. We assumed that basal levels of lipid and protein were those mean amounts remaining at the hatching stage when those components were at lowest levels for the reproductive season, in the year when levels were lowest (i.e., 1979). Yields of 37.7y kJ/g lipid and 18.0 kJ/g protein were used in calculation of energy yield from catabolism of reserves (Ricklefs 1974).

CALCULATION OF DAILY ENERGY EXPENDITURE

We followed Raveling's (1979b) procedure, using the Aschoff and Pohl (1970) equation for basal metabolic rate (BMR) : BMR (kJ/day) = $308 \, W^{0.734}$; W = body mass in kg. Energy used during migratory flight was estimated at 12 times BMR (Raveling and LeFebvre 1967), and for the remainder of the migratory period and the prelaying and laying periods at 3.0 times BMR (estimated from a low of 2.3 to 2.5 times BMR for spring staging Greater Snow Geese [Gauthier et al. 1983] and a high of 3.4 times BMR in King [1973]), and for incubation at 1.25 times BMR (Aschoff and Pohl 1970, King 1973). The cost of adding tissue was the energy content of the tissue (39.57kJ/g lipid, 23.66 kJ/g protein) (Ricklefs 1974) plus the cost of conversion at 70% efficiency (1.43 × energy content) (King 1973). Specific dynamic action and digestive efficiency are accounted for in the metabolic rate equations for each period. Following Raveling (1979b), efficiency of converting endogenous lipids and protein into a clutch of eggs was assumed to be 77% (Brody 1945). Additional energy costs during egg laying included the cost of new tissue (not accounted for by declines in carcass components) deposited in eggs at a conversion efficiency of 70%. However, we assumed that lipid acquired during the prelaying period was added directly to developing follicles and did not require an additional conversion factor. Protein acquired during prelaying and used during laying did have a cost of conversion (77%, Brody 1945), because most protein is added to eggs during laying (King 1973, Ricklefs 1974). Formation of an average clutch of 5.6 eggs (see Results) required 20 days (12 days for rapid maturation of follicles (RMF) (Grau 1976), 8 days for laying of the clutch at a rate of 1 egg/1.5 days). Protein content calculated as above for an average clutch was more than the average amount of protein lost during egg laying. Thus, the energy cost of synthesis of the

additional protein was added to the daily energy requirements during egg laying. The contribution of reserves to meeting daily energy requirements was estimated as the energy yield of the decrease in energy reserves averaged over the number of days in a period. The remaining energy not accounted for by reserves was assumed to be provided from exogenous sources. When reserves increased, all energy requirements were assumed to be supplied from metabolism of food.

Unlike lipid depots, all endogenous protein is dynamic (Kreutler 1980), and cannot accurately be considered a depot of secluded nonfunctional protein. We have used the term "protein reserves" to mean:

". . . those tissue proteins that can be reversibly depleted and repleted, thereby contributing to the free amino acid pools of each cell for the synthesis of certain essential proteins that may be needed for maintenance of cellular integrity during periods of malnutrition or stress" (Wannemacher and Cooper 1970:122).

STATISTICAL ANALYSES

Sample sizes for all analyses are given in Table 1 unless otherwise indicated. For analyses of body mass, carcass components and energy reserves we began with 2-way analysis of variance (ANOVA) (PROC GLM, SAS 1988) to determine year, stage of reproduction and interaction effects. When there were only stage effects, we used a 1-way ANOVA with Duncan's multiple range tests to determine differences between stages of reproduction. When there were significant ($P \leq 0.05$) year or interaction effects, we examined between stage and between year differences with t-tests of least squares means. Because year or interaction effects frequently accounted for a very small proportion of the variation relative to stage of reproduction, we combined years where indicated when discussing general relationships. Nevertheless, annual measures by stage and year are also reported.

We examined the effect of structural size on protein and lipid components of pre-laying, mid-laying and post-laying geese, by doing a Principal Components Analysis (PCA) on 8 morphological measurements (total tarsus, diagonal tarsus, midtoe, culmen, nares to tip of culmen, wing chord, bill nail width and keel, in order of loadings from highest to lowest) for each goose where data were available ($n = 135$) as demonstrated

TABLE 1.   Numbers of adult female Dusky Canada Geese collected in the Willamette Valley, Oregon and on the Copper River Delta, Alaska, 1977–1979.

Stage of reproduction	1977		1978		1979		All years
	n	Date	n	Date	n	Date	n
Premigration	6	4–13 Apr	14	3–13 Apr	16	5–13 Apr	36
Arrival	16	15–21 Apr	12	16–30 Apr	15	16–22 Apr	43
Pre-laying	7	3–8 May	10 (9)[a]	5–13 May	8 (7)	29 Apr–5 May	25 (23)
Mid-laying	2	5 May	1	13 May	3	6–7 May	6
Post-laying	5	7–8 May	0	—	6	6–16 May	11
Hatching	15	5–15 Jun	14	7–15 Jun	10	7–12 Jun	39
Totals	51		51		58		160

[a] Sample sizes for analyses using reproductive tissues (lipid and protein) and for carcass lipid in 1978 were smaller in these cases due to damage from shot.

in Ankney and Afton (1988). We used PC_1 scores as a measure of body size and regressed protein and lipid on PC_1. PC_1 accounted for 43% of the total variation in the data (eigenvalue = 3.46), which we interpreted was due to body size. Subsequent regressions with carcass components yielded a significant relationship with protein in 1977 only. Residuals from this regression (1977 only) were used to recalculate protein scaled to body size (Ankney and Afton 1988), then used in examining relationships of carcass protein to reproductive protein.

A subsequent PCA was done using the four morphological measurements which loaded highest ($n = 135$, PC_1 accounted for 56% of the variation, eigenvalue = 2.25), and the PC_1 scores from this run were subjected to ANOVA (Proc GLM, SAS 1988) to test for differences in structural size of geese collected in different years and stages of reproduction. There was no difference in size of geese between years and stages ($F = 0.77$, $P = 0.69$, df = 134), so we did not scale carcass components to an index of body size for between year and stage comparisons.

We measured the changes in carcass components at each stage of reproduction, and compared these to estimated daily energy requirements to determine the proportion of energy and nutrients that must be provided from exogenous sources. Changes between stages and years were compared to examine variations in patterns of energy use within and between stages and years of reproduction.

RESULTS

PHENOLOGY AND COLLECTIONS

Phenologically, the three years of the study were early on the nesting grounds. Winter weather on the CRD was mild, with little snow and ice accumulation. Snow melt was complete on 22 April, 14 April and 25 April in the three years respectively. Prostrate willow (Salix arctica), sedges (Carex spp.), horsetail (Equisetum spp.) and forbs on the study area responded with early emergence of leaves and shoots. Though not readily obvious, early shoots of food plants were available to geese upon their arrival on the breeding grounds, and access to nest sites was unrestricted by snow within a few days of peak arrival dates (17–22 April 1977, 14–20 April 1978 and 18–25 April 1979). Nesting chronology of geese was similar each year, as were dates of collections of geese keyed to reproductive events (Fig. 2, Table 1). The temporal pattern of nest initiation was not the same in all years (Fig. 2, Median χ^2 = 61.9, $n = 460$, $P < 0.001$), but geese were highly synchronized in initiation of nests (Fig. 2). Geese were earliest and most synchronized in 1977 when 48% of nests were initiated in a four-day period, compared to 1978 and 1979 when geese initiated 35 to 37% of nests on 4–7 May each year. During the study, geese began laying eggs as early as has been recorded for the population (Trainer 1959, Timm and Havens 1973, Bromley 1976, Campbell 1990). Clutch size did not differ by year, and averaged 5.6 eggs overall ($n = 650$). Eggs weighed during laying and early incubation averaged 144 g ($n = 374$). While springs were early, weather was mild and clutch sizes were large, nest success was highly variable. Apparent nest success was 85% in 1977, 54% in 1978 and 17% in 1979 ($n = 112$, 172 and 139 respectively). The rate of nest predation increased throughout the study, particularly by brown bears (Ursus arctos) as predicted due to indirect effects of the Alaska earthquake of 1964 on plant succession (Bromley 1976, see also Campbell 1990).
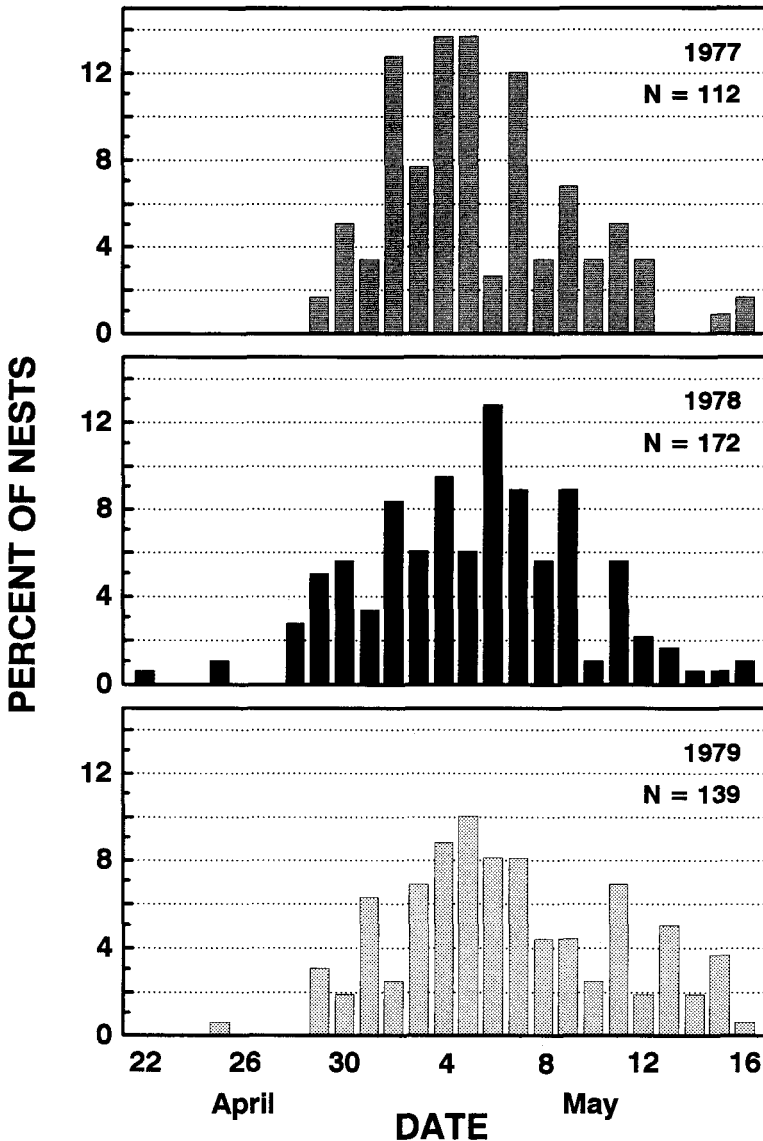
FIGURE 2.   Patterns of nest initiation by Dusky Canada Geese on the Copper River Delta, Alaska, 1977 to 1979.

BODY MASS AND WATER

Body mass varied by stage of reproduction ($P = 0.0001$), but not by year. Mean body mass peaked at pre-lay and was at the minimum by hatch (Fig. 3, Appendix 1). A mean loss of 378 g (10.8%) occurred during migration, followed by a gain of 458 g (15.6%) during prelaying, a loss of 358 g (9.9%) during laying and a loss of 769 g (23.6%) during incubation. Loss from pre-laying to

hatching was 1,127 g (31.1%) in 34 days. The gain in mass during the prelaying period was accounted for by increases in all components.

Water was the major carcass component (Fig. 3, Appendix 1), accounting for 51 to 71% of carcass mass. Water content varied over all stages ($F = 29.8, P = 0.001$ with Duncan multiple range test, $P = 0.05$). Water increased during migration and prelaying periods to a peak of 1,988 g and subsequently declined to 1,601 g by hatching.
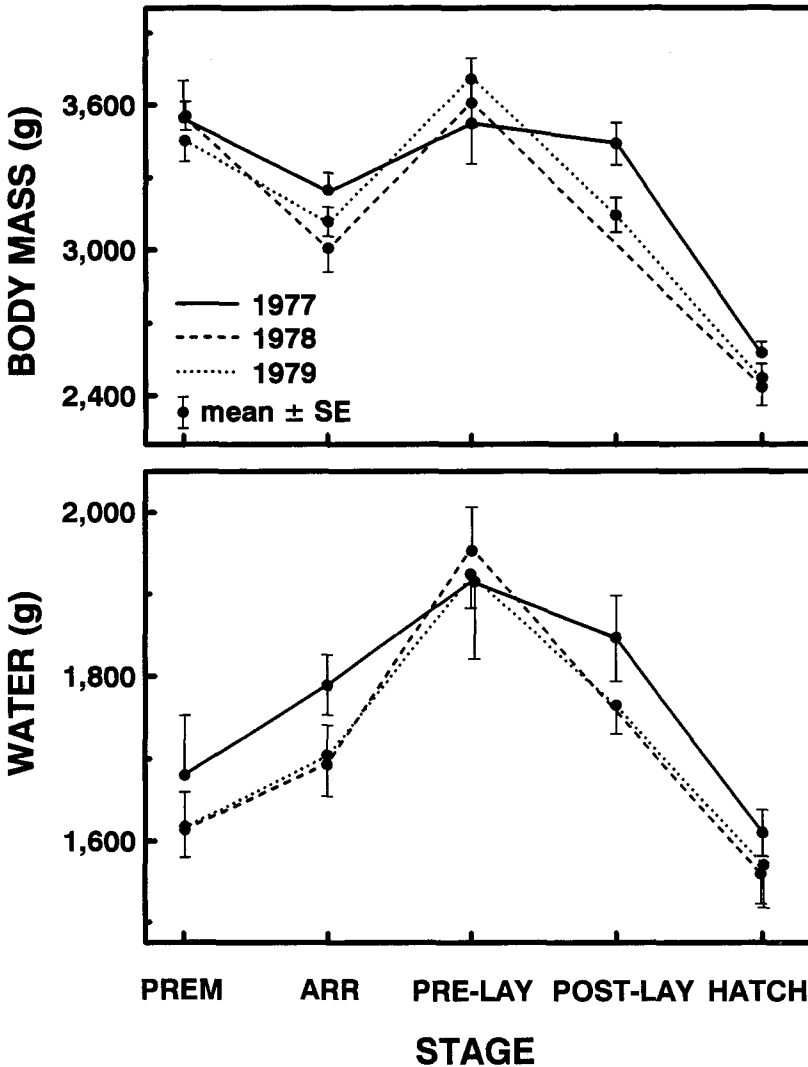
FIGURE 3.   Patterns of change in body mass and carcass water of adult female Dusky Canada Geese, 1977 to 1979.

Increases in water accounted for 55 to 78% of mass gain during prelaying.

LIPID AND PROTEIN

Carcass lipid varied over stages of reproduction ($P = 0.0001$) with some interaction between year and stage ($P = 0.005$). However, little variation in lipid was accounted for by interaction ($F = 3.1$) relative to stage of reproduction ($F = 239.7$) and t-tests of least squares means for year indicated no differences between years. Thus, both annual amounts and lipid combined over years

are presented (Fig. 4, Table 2). Lipid declined dramatically during migration (435–608 g, $P < 0.05$). Lipid accounted for all mass loss during migration, and 62% of mass loss during incubation.

Carcass protein (Fig. 4, Table 2) varied by year ($F = 22.2$, $P = 0.0001$) and stage of reproduction ($F = 37.6$, $P = 0.0001$). Protein was consistently highest at all stages in 1977, lowest in 1979 and intermediate in 1978 ($P < 0.007$). Levels of protein did not change during migration ($P > 0.5$), although annual differences were more pro-

TABLE 2. Mean body mass (g) carcass component mass (g) and energy reserves (kJ × 10³) of adult female Dusky Canada Geese collected in the Willamette Valley, Oregon and on the Copper River Delta, Alaska, 1977–1979. Standard errors are given in parentheses following means.

Component (year)	Stage of reproduction				
	Premigration	Arrival	Pre-laying	Post-laying	Hatching
Body mass (all)	3,512 (46)[a]	3,134 (43)[b]	3,622 (62)[a]	3,264 (68)[b]	2,495 (30)[c]
Water (all)	1,626 (24)[a]	1,733 (20)[b]	1,935 (32)[c]	1,801 (31)[b]	1,582 (21)[a]
Lipid (1977)	961 (28)[a]	526 (35)[b]	495 (54)[b]	563 (21)[b]	75 (10)[c]
Lipid (1978)	1,044 (40)[a]	436 (45)[b]	442 (40)[b]	–	59 (7)[c]
Lipid (1979)	894 (49)[a]	500 (27)[b]	559 (35)[b]	423 (25)[c]	48 (5)[d]
Lipid (all)	963 (29)[a]	492 (21)[b]	494 (26)[b]	486 (27)[b]	62 (5)[c]
Protein (1977)[A]	588 (22)[a]	562 (11)[a]	617 (31)[b]	575 (11)[a]	498 (10)[c]
Protein (1978)[B]	517 (11)[a]	527 (16)[a]	613 (14)[b]	–	458 (10)[c]
Protein (1979)[C]	515 (9)[a]	485 (13)[a]	584 (18)[b]	495 (12)[a]	431 (14)[c]
Energy reserves (1977)[A]	36.7 (1.21)	20.4 (1.37)	20.2 (2.43)	22.0 (0.91)	2.2 (0.46)
Energy reserves (1978)[AB]	39.1 (1.58)	16.3 (1.91)	19.2 (1.50)	–	0.9 (0.40)
Energy reserves (1979)[A]	33.4 (1.90)	18.0 (1.10)	21.9 (1.47)	15.3 (0.36)	0 (0.39)
Energy reserves (all)	36.2 (1.13)	18.4 (0.85)	20.4 (1.01)	18.3 (1.20)	1.18 (0.28)

Change in superscripts (lower case for stages, uppercase for years) indicate significant differences ($P \leq 0.05$) between all pair combinations from an ANOVA (see Methods).

nounced by arrival on the CRD. Protein increased 55–99 g during prelaying ($P = 0.05$), and decreased 42–89 g during laying ($P = 0.05$) and 64–77 g during incubation ($P = 0.05$). During prelaying periods, protein levels increased the most (99 g) in 1979 when levels were lowest, and the least (55 g) in 1977 when levels were the highest. Increases in protein accounted for 20–33% of mass gain during prelaying on the breeding grounds.

ENERGY RESERVES

Energy reserves varied by stage of reproduction ($P = 0.0001$), and year ($P = 0.05$), with interaction ($P = 0.03$); however, year and interaction accounted for relatively little variation ($F = 3.2$ and 2.3 respectively, compared to $F = 229.3$ for stage). Energy reserves were greater in 1977 than in 1979 ($P < 0.007$), but neither year was significantly different from 1978 ($P > 0.15$). Reserves were greatest during premigration, similar during prelaying and laying, and lowest at hatching (Fig. 5, Table 2). Lipid accounted for the major proportion of energy reserves (i.e., lipid above 48 g, the minimum amount remaining at hatch) throughout the reproductive season (Fig. 5), except at hatching when we assumed all reserves had been depleted. Protein reserves (amounts above 431 g, the minimum amount remaining at hatch) peaked at the prelaying stage, then decreased through laying and incubation (Fig. 5), but never represented more than 18%

of energy reserves. Although mean energy reserves generally declined over the reproductive season, in 1978 and 1979 they increased by 2,805 and 3,906 kJ respectively during the prelaying period (Fig. 5, Table 2). During 1978 and 1979, lipid accounted for 44% and 57% of the increase respectively, while protein accounted for 56% and 42% respectively, of the increase in caloric reserves measured during prelaying. Migration was the most costly period, followed by incubation, then laying (Fig. 5). Energy reserves increased by 9% (not significant) in 1977 during laying, and decreased by 30% in 1979.

MATURATION OF FOLLICLES

Evidence of the timing of RMF was observed in the size of the largest follicle in geese collected at the arrival stage on the delta. The average size of the largest follicle in geese collected between 15 and 21 April (Table 3) indicated a slow rate of growth ($\bar{x} < 0.09$ mm/day) until 20 April when the growth rate increased sharply to >2 mm/day. Projecting a growth rate of 2.3 mm/day for 13 days from an average largest follicle size of 12.4 mm on 20 April (Table 3), a follicle diameter of 42.3 mm would be expected by 3 May. This projection was consistent with a follicle diameter of 43–44 mm typical of Dusky Geese at ovulation (unpubl. data) and with the peak of initiation of laying on 4 to 7 May. Thus geese began RMF about the time of their arrival on the nesting grounds or shortly thereafter.
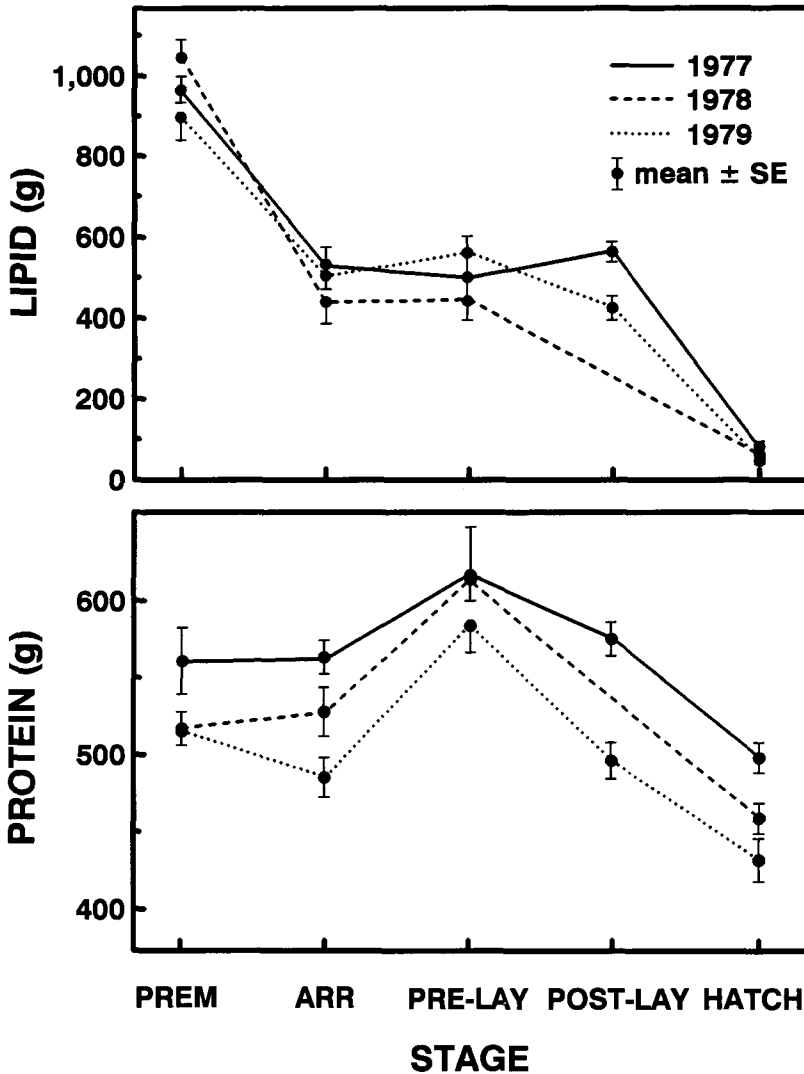
FIGURE 4. Patterns of change in carcass lipid and protein of adult female Dusky Canada Geese, 1977 to 1979.

DECLINE OF RESERVES
DURING EGG LAYING

Over the laying period, carcass protein declined by 1.87 g in 1978 and 0.72 g in 1979 for each 1.0 g of protein deposited in reproductive (ovary, oviducal and oviposited eggs) tissue (Fig. 6). In 1977, the year when overall protein levels were highest throughout the season, the average total decline in protein of 42 g during the laying period was not significant. Over all years, the range of carcass protein was smaller at each subsequent stage of laying, from pre-laying (range of 199 g),

to mid-laying (range = 167 g) to late laying (range = 141 g), and to post-laying (range 123 g), apparently an increasing conservation of protein reserves to similar levels at the beginning of incubation.

Carcass lipid declined by 1.9 g per g of reproductive lipid tissue formed over all years (Fig. 6); however, this relationship was weak ($r^2 = 0.20$). On an annual basis, lipid did not change during laying in 1977 ($P = 0.73$), while they declined steeply in 1978 (5.6 g per g reproductive tissue) and 1979 (2.6 g per g, Fig. 6).
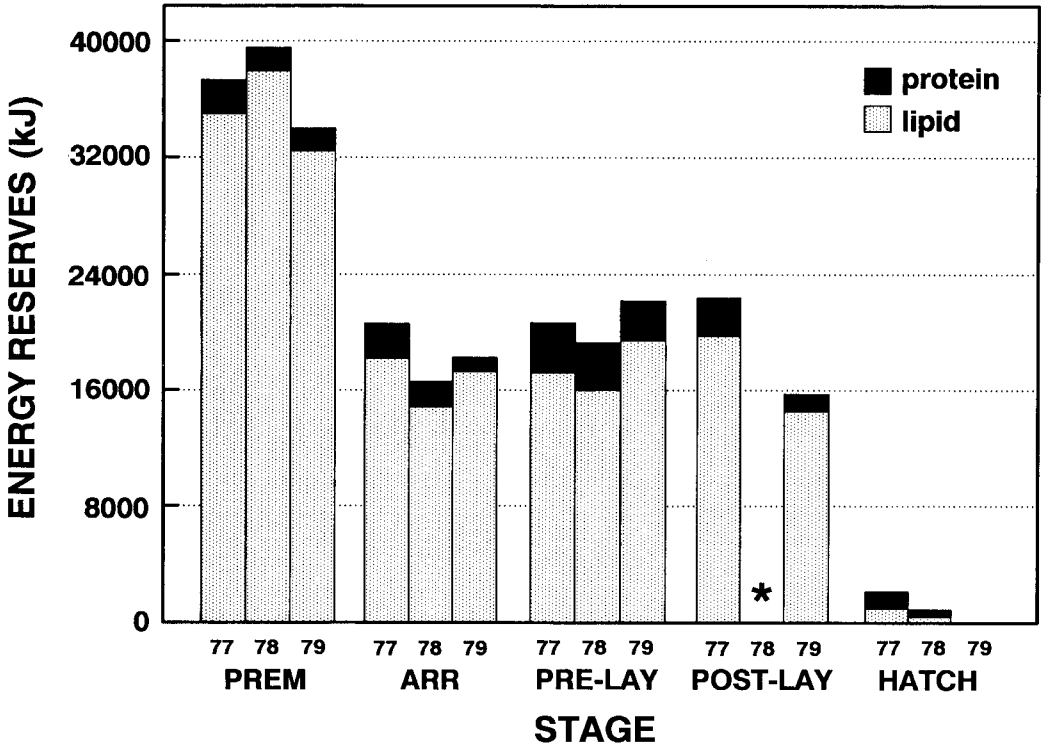
FIGURE 5.   Energy reserves of adult female Dusky Canada Geese throughout the reproductive season, with relative contribution of lipid and protein, averaged for 1977 to 1979. The * indicates missing data for 1978.

For geese collected in 1977, a significant relationship between carcass protein and PC_1 scores (indices of body size), was detected ($y = 601 + 16.2x$, $r^2 = 0.30$, $P = 0.05$, $df = 10$). A subsequent regression of corrected protein (adjusted for body size) on reproductive protein indicated no relationship ($P = 0.97$), in agreement with the re-

TABLE 3.   Average largest follicle size for 30 Dusky Canada Geese collected on the Copper River Delta, Alaska, 1977–1979.

Date	Mean largest follicle diameter in mm (n)	Difference in follicle size from previous day
April		
15	6.9 (2)	—
16	7.5 (6)	0.6
17	8.9 (3)	1.4
18	—	(0.7)[a]
19	10.2 (6)	(0.7)[a]
20	12.4 (7)	2.2
21	14.9 (6)	2.5

[a] These are average daily differences determined from the difference between 19 and 17 April, since no sample was obtained on 18 April.

gression of uncorrected carcass protein by reproductive protein. No other relationship between carcass components and indices of body size was detected.

ROLE OF ENDOGENOUS RESERVES AND FOOD IN MEETING DAILY ENERGY REQUIREMENTS

Average energy requirements estimated for each period of reproduction ranged from a high of 3,438 kJ/day during prelaying to a low of 837 kJ/day during incubation (Table 4). Energy reserves varied in importance during the four periods of reproduction. Requirements during migration were met almost equally by catabolism of lipid reserves and of food. During the prelaying period, food provided all of the energy and nutrient needs of geese. Energy reserves utilized during laying provided only 7% of daily energy needs (2,630 kJ, Table 4), but reserves played a major role in meeting energy requirements during the incubation period (Table 4). Reserves were expended largely during migration and incubation, were maintained during prelaying, and
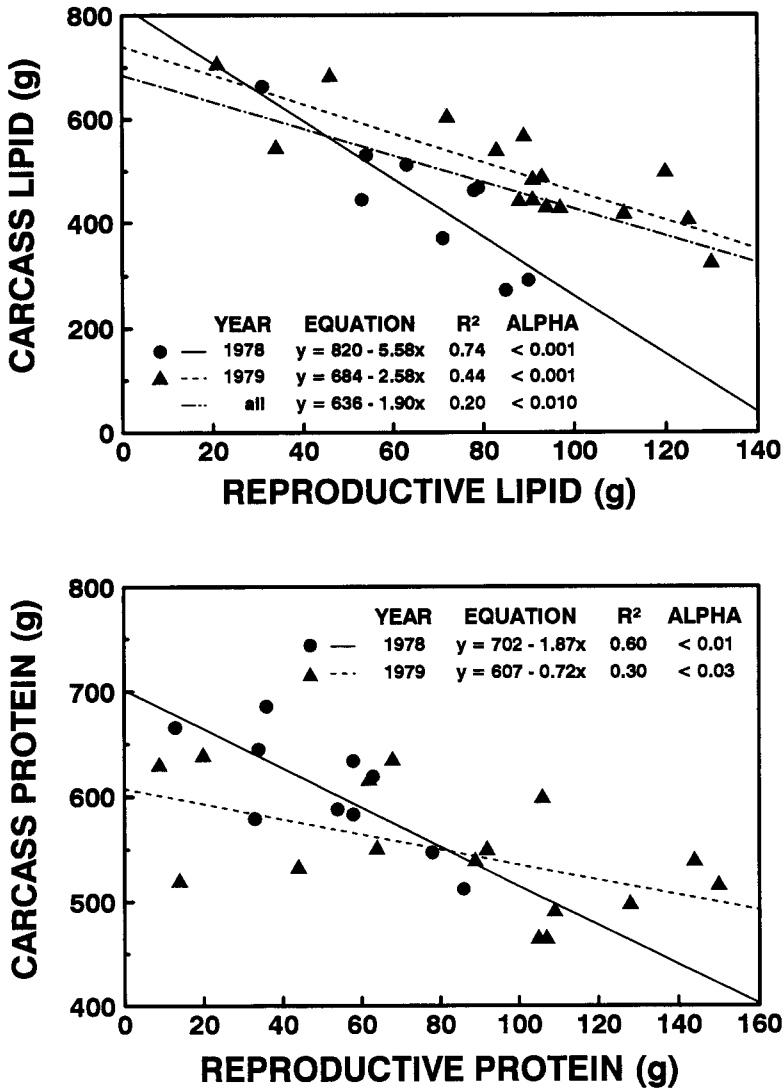
FIGURE 6. The relationship of declining carcass lipid and protein to the increasing allocation of lipid and protein to reproductive tissues (ovary, oviducal egg and oviposited eggs), in pre-lay, mid-lay and post-lay adult female Dusky Canada Geese.

were expended slightly more during laying than was acquired the previous period. Reserves acquired on the wintering grounds were important throughout the reproductive season (except during prelaying) whereas those derived on the nesting grounds were utilized during egg laying and incubation (Table 4).

DISCUSSION

There are two possible sources of error of which we are aware. First, due to the early springs and generally favorable conditions throughout the three years of this work, our results may not reflect the average or more severe situations Dusky Geese can experience, at least on the nesting grounds. During later springs, geese may rely more on endogenous reserves and less on food, but we did not have the opportunity to assess this. Secondly, because this study was conducted prior to the establishment of certain procedures now commonly followed, direct comparison with other work must take into account two different

TABLE 4. Average contribution of endogenous and exogenous energy sources to daily energy requirements of adult female Dusky Canada Geese during four periods of reproduction.

Reproductive period	Number of days	Body weight (kg)		Daily[a] energy needs (kJ)	Mean daily change				Contribution from reserves		Contribution from food	
					In reserves		In reprod. tissues					
		Range	Midpoint		Lipid (g)	Protein (g)	Lipid (g)	Protein (g)	Energetic yield (kJ)	% of daily needs	kJ	% of daily needs
Migration	11	3.51–3.13	3.32	3,243	−43.0	0	—	—	1,620	50.0	1,623	50.0
Prelaying	11	3.13–3.62	3.38	3,438	+5.8	+11.5	+5.6	+4.3	0	0	3,438	100.0
Egg laying	8	3.62–3.26	3.44	2,630	−1.0	−8.2	+5.2	+9.0	185	7.0	2,445	93.0
Incubation	27	3.26–2.49	2.88	837	−15.7	−2.6	—	—	636	76.0	201	24.0

[a] Daily energy requirements were calculated as: migration 12 times BMR for 40 hr, assuming migration of 2,560 km and flight speed of 64 km/hr, 3.0 times BMR remainder of migration; prelaying, 3.0 times BMR plus tissue for storage and ovarian development; egg laying, 3.0 times BMR plus conversion of reserves to egg reproduction, plus new tissue synthesis for egg production; incubation, 1.25 times BMR (see Methods).
[b] Food was assumed to provide that part of a goose's daily energy requirements not accounted for by a loss in endogenous reserves.

methodologies. The inclusion of the oviduct in our measure of carcass composition is now considered unusual. However, because carcass tissues actually increased during the prelaying period when the oviduct would undergo most development, the only cost we did not account for was the possible cost of conversion from stored reserves to oviducal tissue. It is more likely that the oviduct developed directly from new tissue added during prelaying so that there was no extra cost not considered in this analysis. A third potential bias was the use of chloroform-methanol in lipid extraction, a solvent mixture that is now known to extract some non-lipid material (Dobush et al. 1985). We are not able to directly assess this factor, but close agreement of results between years and with other studies indicates the error was likely not significant. Changes in total lipid were generally gross changes, such that the total effect of the error would not change the conclusions of the study. The predicted error would result in an overestimate of lipid, which would lead to underestimating the importance of exogenous energy sources. Dobush et al. (1985) note that the error in estimates would be proportionately greatest when lipid content was low, such as at hatching in this study. Because our primary conclusion relating to lipid reserves at hatch was that they were extremely low, such error would have little effect on our conclusions. Independent samples of homogenate were used for determination of protein content, so that the chloroform-methanol extractions did not affect these measures.

Nesting success declined over the course of the study. Nest initiation dates tended to be earlier in 1977 and later in 1978 and 1979. Further, constancy of incubation was greatest in 1977 (92.9%) and lower in 1978 and 1979 (85.1 and 87.9% respectively, RGB unpubl. data). It is possible that this may be related to the progressively lower amounts of lipid and protein reserves observed at post-laying and at hatching over the three years. Geese may delay nest initiation pending the accumulation of higher protein reserves (Reynolds 1972, Jones and Ward 1976, Fogden and Fogden 1979, Wypkema and Ankney 1979), and they may be forced to take more time off nests during incubation to supplement reserves, thereby exposing nests to predators (Sherry et al. 1980, Le Maho et al. 1981, Aldrich and Raveling 1983, Bromley 1984). However, because of the disturbed environment produced

by the 1964 earthquake, plant succession, and an invasion of brown bears as major nest predators on the CRD (Bromley 1976, Campbell 1990), we were not able to assess this possibility. Bears may be able to find and depredate nests with similar efficiency regardless of the presence or absence of the goose, unlike most avian predators against which geese in good condition can normally defend their nests. Possible variation in feeding conditions from year to year offers an alternative explanation of decreased constancy and reproductive success.

Body mass changed by stage of reproduction but not by year, despite the fact that one important constituent, protein, did vary by year. While body mass declined by 11% during migration, energy reserves declined by 52%. A peak in body mass occurred at initiation of egg laying when energy reserves were 43% below the peak. These relationships indicate that the use of body mass alone as an index to condition of geese must be used with caution, and only within a stage of reproduction and not between stages.

MIGRATION

Rather than peaking near the end of migration as predicted, lipid content of adult female Dusky Canada Geese reached a peak for the entire reproductive season at premigration. Fat content of premigrating female Dusky Geese (29.8%) was similar to that of female Giant Canada Geese (*B. c. maxima*) at 29.0% (McLandress and Raveling 1981). Similarly, fat accumulation in premigratory Brant, albeit only 12% lipid, was considered substantial by Vangilder et al. (1986). In contrast, Interior Canada Geese (*B. c. interior*) and Cackling Canada Geese (*B. c. minima*) gained little or no weight before migration (Raveling and Lumsden 1977, Raveling 1979b). During migration, Dusky Geese depleted their lipid reserves by 52% (473 g), the highest rate of energy reserve use in all periods in the reproductive season. Lesser Snow Geese (*C. c. caerulescens*), Ross' Geese (*C. rossii*), and Cackling and Interior Canada Geese all experience weight gains during spring migration, and arrive on nesting grounds at near peak body weights (Barry 1967, Raveling and Lumsden 1977, Ankney and MacInnes 1978, Raveling 1979a). Brant, however, do not appear to change weight during spring migration (Vangilder et al. 1986), and White-fronted Geese appear to conform to the pattern observed in Dusky Canada Geese. For example, average loss of lipid

for adult female White-fronted Geese, comparing premigration samples one year to arrival samples in two other years, was 30.8 to 71.4% of crude lipid in the carcass (our calculations from Ely and Raveling 1989 and Budeau et al. 1991). Raveling and Lumsden (1977:49) concluded that the: "energy cost of long distance migration for birds as large as a Canada Goose is relatively small and is not the major evolutionary factor demanding large fat stores in spring." Dusky Canada Geese do not conform to that pattern.

The migration route of Dusky Geese is 2,600 km long and lies largely along coastal Washington, British Columbia and southeastern Alaska. Because of the maritime climate, geese are able to migrate quickly, without awaiting the 0°C isoclines as do some geese in the interior of the continent (Ryder 1967, Cooper 1978). Based upon the dates of major exodus from winter refuges and arrival on the nesting grounds (RGB and RLJ pers. observ.), the average migration period of Dusky Geese is about 11 days. The fiord-like terrain enroute provides few staging areas with high quality forage (see Isleib 1979, Pitelka 1979), unlike the abundant, high quality staging opportunities available to interior geese (cf. Raveling and Lumsden 1977). Thus, Dusky Geese complete migration quickly, apparently stopping little along the way. In contrast to the migration route, the wintering grounds of Dusky Geese offer abundant food resources and a mild climate. Dusky Geese take advantage of this situation by accumulating reserves on the wintering grounds to meet a large proportion of the energy needed during migration and the reproductive season. Greater Snow Geese exhibit a similar pattern (G. Gauthier, pers. comm.).

The three early springs characterizing the study had similar phenological conditions, yet geese had different levels of protein reserves and, in at least two of the three years, different energy reserves. Weather was similar and seemingly favourable each year during spring on the wintering grounds. Geese left the Willamette Valley with similar reserves each year, but pronounced differences between years were apparent in protein reserves upon arrival on the CRD. Apparently, geese met varying annual staging or migrating conditions while enroute north. While considerable use of lipid reserves occurred during migration, we estimated that an approximately equal amount of energy was derived from

exogenous sources. Thus, food remains important for both energy and protein needs during this period. Based on the characteristics of the spring migration of Dusky Geese, and the variation in reserves upon completion of migration, we suggest that the energy cost of migration influences the overall energetic strategy of reproduction evolved by geese. Patterns of energy use evolve not only in response to environmental conditions on the breeding grounds during the prelaying, laying and incubation periods, but also in response to length and duration of migration and environmental conditions on migration and wintering grounds.

PRELAYING AND LAYING PERIODS

The prelaying period during all years for Dusky Geese was 13 to 18 days, equal to or longer than the period of RMF (Grau 1976). Raveling (1978) suggested that Canada Geese initiated RMF upon departure from the last major staging grounds or upon arrival on the breeding grounds. Similar to White-fronted Geese in coastal Alaska (Ely and Raveling 1984, Budeau et al. 1991) and Greater Snow Geese on Bylot Island, Northwest Territories (Gauthier and Tardif 1991), Dusky Geese initiated RMF immediately after arrival on the CRD possibly because early spring thaws made food and nest sites available. The ability of Dusky Geese to delay RMF after arrival during years of late spring thaws is unknown. For Dusky Geese, which at least during early springs depend upon food protein for supplementing reserves and for egg formation during the prelaying and laying periods, the ability to postpone RMF until a protein rich food source becomes available may be adaptive. The timing of spring snowmelt on the CRD is highly variable (Timm and Havens 1973, Bromley 1976), and requires Dusky Geese to adapt to resulting variation in availability of food and nest sites. The long growing season on the CRD may permit geese to delay RMF until suitable conditions exist for the acquisition of exogenous protein required in egg formation. This opportunity is likely constrained, however, by energy and nutrient availability relating to forage quality during the brood rearing period (see Sedinger and Raveling 1986).

In contrast to our prediction of a loss of reserves, Dusky Geese were able to maintain or increase lipid reserves and increase protein reserves during the prelaying period on the breeding grounds, indicating considerable use of exogenous nutrient sources. Most geese are generally thought to experience a loss of reserves during the prelaying period (Barry 1962, 1967; Hanson 1962; Newton 1977; Raveling and Lumsden 1977; Raveling 1978, 1979b; and others), but little quantitative evidence is available. Barry (1967) recorded weight loss in Brant and Lesser Snow Geese after arrival on nesting grounds. Most workers did not compare the composition of geese at the beginning and end of the prelaying period on the breeding grounds (Ankney and MacInnes 1978; Raveling 1979a, 1979b; Thomas 1983; Ankney 1984). However female Greater White-fronted Geese maintained lipid reserves while increasing carcass protein during prelaying on the Yukon-Kuskokwim Delta, Alaska (Budeau et al. 1991), and Greater Snow Geese maintained lipid and protein reserves on high arctic breeding grounds during prelaying while egg formation was occurring (Choiniere and Gauthier 1992).

The use of food on the nesting grounds for maintenance of lipid reserves and acquisition of protein may be more typical than has been previously thought. Thomas (1983) determined that at least some of the protein required for egg formation in Lesser Snow Geese at a southern colony must have been derived from food. Bromley (1984) concluded that significant food resources were available during prelaying and laying periods even on arctic breeding grounds, and predicted that arctic nesting geese would make use of these resources. Lesser Snow Geese gained weight even when their northern staging area was still covered by snow and ice (Prevett et al. 1985). Thus, even in a late spring, we expect that Dusky Geese would be able to supplement endogenous reserves to some extent. Studies of feeding time by female geese near the northern limits of their breeding range also reflect the potential for gathering of nutrients during the prelaying period. For example, both Greater White-fronted Geese and Greenland White-fronted Geese (*A. a. frontalis*) fed 68% of the time during prelaying on the North Slope of Alaska and in West Greenland (S. G. Simpson, pers. comm.; Fox and Madsen 1981), respectively. Similar observations are 75% for Greater Snow Geese on Bylot Island, Northwest Territories (Gauthier and Tardif 1991); and 59 to 75% for both Greater White-fronted Geese and Richardson's Canada Geese (*B. c. hutchinsii*) respectively in the central Canadian Arctic (RGB unpubl. data).

The predicted loss of lipid reserves during lay-

ing was smaller than expected, and did not occur in 1977 (Fig. 5). In 1978 and 1979, lipid reserves did decline during laying, at a rate of 2.6 to 5.6 g/g of reproductive lipid tissue (Fig. 6). However, in 1978 the mid- to post-laying stages were not well represented in samples collected. Because nutrient demands for egg formation are much higher during early laying than during late laying (Gilbert 1971, King 1973), it is likely that the rates of reserve loss (Figs. 5, 6) were overestimated for that year. Nevertheless, the laying period was energetically costly (Table 4), indicating a large expenditure of energy other than for lipid deposition in eggs. Perhaps increased feeding activity to meet heavy protein demands during laying, in concert with territorial and nest defense activity, combined to raise energy costs during this period. Despite the decline in lipid reserves, considerably energy must have been derived directly from food to meet daily requirements during laying. There was an obvious drain on endogenous protein of Dusky Geese as laying progressed and commitments to reproductive tissues increased (Figs. 5, 6). Geese lost 42–89 g of protein, which was 7–15% of their total protein content, but which represented 23–58% of their protein reserves (protein above the base level of 431 g). Lesser Snow Geese and Brant lost 21% and 20% respectively of total protein content from the prelaying period to early incubation (calculated from Ankney and MacInnes 1978 and Ankney 1984). These losses represented 59% and 86% of protein reserves of Snow Geese and Brant respectively. In another study of Lesser Snow Geese, females lost 52.5 g of protein between arrival and post-laying (Thomas 1983). Despite differences in methodology, it is apparent that a major use of protein reserves occurs during laying.

Unlike lipid reserves, protein reserves during prelaying and laying periods were quite dynamic, with significant changes during both periods each year. In addition, carcass protein was consistently highest in 1977, the only year that protein was related to PC_1 scores indexing body size during the laying period. In 1978 and 1979, carcass protein was lower and not related to body size. One explanation of the fit in 1977 is that protein content was at or near maximum for most individual geese that year, and thus related to body size, whereas in subsequent years it varied more according to individual capabilities to accumulate reserves (Teunissen et al. 1985), for which

body size may be a poor measure (Black and Owen 1989). Protein gains during prenesting were small in 1977 when levels were high, but were much greater in 1978 when levels were moderate and greatest in 1979 when levels were lowest, possibly indicating an ability to partially compensate for the lower protein reserves (Fig. 4). Similarly, the decline in protein during laying was moderate in 1977 (42 g), and more than double in 1979 (89 g) when levels were lowest. The tendency for variation in carcass protein to decrease as laying progresses is consistent with the findings of Raveling (1979a) and Thomas (1983) for Cackling Canada Geese and Lesser Snow Geese respectively. Perhaps the considerable protein demands during egg laying (Gilbert 1971) saturates the ability of the bird to mobilize or consume necessary amino acids, and thereby becomes a factor in the cessation of follicular development during laying.

The loss of 42–89 g of protein during laying accounted for 35–75% of the protein content in an average clutch of eggs. Since much of the egg protein is contributed during the 24–48 hr immediately before laying (Gilbert 1971), a major portion of egg protein was derived directly from food during the laying period. Buschbaum and Valiela (1987) demonstrated high selectivity of breeding Canada Geese for high dietary nitrogen. Rockwell et al. (1987) observed that Lesser Snow Geese regularly lay clutch sizes below their optimal clutch, and speculated that a substantial proportion of the unexplained variation in clutch size may derive from proximate factors related to food acquisition. Use of food by geese might explain other poorly understood variations in clutch size and egg size relationships (e.g., Hamann and Cooke 1989, MacInnes and Dunn 1988, Rohwer 1988). We concluded that Dusky Geese were able to attain nutrients required for maximum clutches throughout this study, but we suspected that endogenous reserves were minimally sufficient to achieve this in 1979.

INCUBATION

As predicted, lipid and protein of female geese declined steeply during incubation. This stage seems to be the most consistently demanding to reserves of many species of geese (Ankney and MacInnes 1978, Raveling 1979a, Le Maho 1983, Mainguy and Thomas 1985, Thompson and Raveling 1987, Murphy and Boag 1989). Geese appear to be in a tenuous state energetically by

the time incubation is complete, with minimal if any reserves remaining. They may starve to death on the nest (Harvey 1971, Ankney and MacInnes 1978, Le Maho et al. 1981), spend increasing time away from the nest to feed (Aldrich and Raveling 1983, Bromley 1984, Murphy and Boag 1989), or completely abandon nests (Ankney and MacInnes 1978, Bromley 1984). All of these consequences lead to decreased survival of offspring. Despite the major loss of endogenous reserves, most geese do take recesses to feed to some degree during incubation (Aldrich and Raveling 1983, Ankney 1984, Bromley 1984, Murphy and Boag 1989, but see Thompson and Raveling 1987), indicating that although food may be a relatively small proportion of daily energy requirements, it may constitute a critical contribution. Geese must retain sufficient lipid reserves to meet energy needs throughout incubation, modified in accordance with their opportunity to take advantage of endogenous sources with minimal risk of egg loss during recesses.

CONCLUSIONS

We reject the hypothesis that exogenous sources of lipid and protein are not important to breeding Dusky Canada Geese, and that variation in endogenous reserves simply reflects demands on them. We found that exogenous sources were important at all stages, accounting for all requirements during the prelaying period, and meeting a small but critical proportion of requirements during incubation. Variation in amounts of endogenous reserves was influenced by energy demands, but also by the degree to which geese used exogenous sources of nutrients. Patterns of energy use will vary between species and among subspecies of geese. Extrapolation between populations that have been studied to those that have not requires caution. We expect that most geese will take advantage of opportunities to supplement endogenous reserves, mediated by availability of high quality forage, expected and recent energy or nutrient demands, and risks to survival and reproductive success associated with procurement of nutrients from exogenous sources.

ACKNOWLEDGMENTS

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APPENDIX 1. Mean body mass (g) carcass component mass (g) and energy reserves (kJ × 10³) by reproductive stage and year of adult female Dusky Canada Geese collected in the Willamette Valley, Oregon and on the Copper River Delta, Alaska, 1977–1979. Standard errors are given in parentheses and sample size in Table 1.

Component (year)	Premigration	Arrival	Prelaying	Mid-laying	Post-laying	Hatching
Body mass (1977)	3,547 (137)	3,245 (66)	3,529 (157)	3,425	3,446 (81)	2,569 (40)
Body mass (1978)	3,556 (58)	3,009 (88)	3,616 (92)	3,076	–	2,436 (51)
Body mass (1979)	3,460 (77)	3,115 (62)	3,701 (74)	3,739 (58)	3,134 (57)	2,467 (69)
Body mass (all)	3,512 (46)	3,134 (43)	3,622 (62)	3,524 (150)	3,264 (68)	2,495 (30)
Water (1977)	1,680 (74)	1,790 (34)	1,916 (84)	1,777	1,846 (52)	1,611 (26)
Water (1978)	1,614 (31)	1,694 (35)	1,957 (50)	1,779	–	1,558 (34)
Water (1979)	1,616 (39)	1,703 (34)	1,923 (36)	1,996 (57)	1,764 (32)	1,572 (56)
Water (all)	1,626 (24)	1,733 (20)	1,935 (32)	1,887 (64)	1,801 (31)	1,582 (21)
Lipid (1977)	961 (28)	526 (35)	495 (54)	362	563 (21)	75 (10)
Lipid (1978)	1,044 (40)	436 (45)	442 (40)	272	–	59 (7)
Lipid (1979)	894 (49)	500 (27)	559 (35)	500 (36)	423 (25)	48 (5)
Lipid (all)	963 (29)	492 (21)	494 (26)	416 (58)	486 (27)	62 (5)
Protein (1977)	558 (22)	562 (11)	617 (31)	596	575 (11)	498 (10)
Protein (1978)	517 (11)	527 (16)	613 (14)	512	–	458 (10)
Protein (1979)	515 (9)	485 (13)	584 (18)	562 (18)	495 (12)	431 (14)
Protein (all)	523 (7)	526 (9)	604 (12)	565 (26)	531 (15)	467 (8)
Energy reserves (1977)	36.7 (1.21)	20.4 (1.37)	20.2 (2.43)	14.8	22.0 (0.91)	2.2 (0.46)
Energy reserves (1978)	39.1 (1.58)	16.3 (1.91)	19.2 (1.50)	9.9	–	0.9 (0.40)
Energy reserves (1979)	33.4 (1.90)	18.0 (1.10)	21.9 (1.47)	19.4 (1.44)	15.3 (0.36)	0 (0.39)
Energy reserves (all)	36.2 (1.13)	18.4 (0.85)	20.4 (1.01)	16.3 (2.50)	18.3 (1.20)	1.18 (0.28)

Stage of reproduction