AN ABSTRACT OF THE THESIS OF

Robert G.H. Bromley for the degree of Doctor of Philosophy

in Wildlife Science presented on June 6, 1984

Title: The Energetics of Migration and Reproduction of Dusky Canada Geese (*Branta canadensis occidentalis*)

Abstract Approved: Redacted for privacy

Robert L. Jarvis

Adult female Dusky Canada Geese were studied on the Copper River Delta, Alaska and in the Willamette Valley, Oregon during April through July, 1977 to 1979. Objectives of the research were to: 1) determine the chronology of use of protein and energy reserves in relation to four periods of reproduction defined as the migration, prelaying, egg laying and incubation periods, and 2) to assess the role of food in meeting energy requirements during these four periods. During the study, 162 geese were collected for composition analysis.

Endogenous lipids were heavily utilized during migration, egg laying and incubation. Endogenous protein was important during egg laying and incubation. Food supplied about half of the energy requirements calculated for the migration period, all needs during prelaying, over 75% during egg laying and about one third of energy requirements during incubation. Food was most important for supplementing high protein needs of laying geese and both protein and energy needs of geese during the last third of the incubation period when endogenous reserves were depleted.

Although northern nesting geese have been assumed to be largely independent of food during prelaying through incubation, it was suggested that food is in fact proximately important, influencing both clutch size and patterns of energy use during incubation. Ultimately, the timing of nesting and clutch size of northern nesting geese may have evolved in response to the need for an optimal food supply about two-thirds of the way through incubation.

THE ENERGETICS OF MIGRATION AND REPRODUCTION OF DUSKY CANADA GEESE

(*Branta canadensis occidentalis*)

by

Robert G.H. Bromley

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements of
degree of
Doctor of Philosophy

Completed June 6, 1984

Commencement June 1985

APPROVED:

Redacted for privacy

Professor of Wildlife in charge of major

Redacted for privacy

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Date thesis is presented June 6, 1984

Typed by E. Irvine for Robert G.H. Bromley

ACKNOWLEDGMENTS

Funding for this research, provided by the Office of Migratory Bird Management, U.S. Fish and Wildlife Service, Washington, D.C. and administered through the Cooperative Wildlife Research Unit, Oregon State University, is gratefully acknowledged. Thanks also to the Oregon Duck Hunters Club for their contribution in 1977.

Logistical support in Alaska was provided by the U.S. Forest Service (Chugach National Forest) and the Alaska Department of Fish and Game, Cordova. In Oregon, the Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, and Willamette Valley National Wildlife Refuges (USFWS) supported the project with field transportation and laboratory supplies and equipment.

Lars H. Holtan provided excellent field assistance and companionship during 1977 on the nesting grounds, and continued to maintain an interest in the work throughout the study. I am particularly indebted to D. Kyle Bynon for his capable and enthusiastic contributions as field assistant in 1978 and for completing the major part of the field work in 1979 after I suffered a broken ankle, with complications, early in the field season. Thanks also for that trip into town Dan! My appreciation is also extended to Lars, Dick Sellers (ADF & G, Anchorage) and others who pitched in to help Dan during my absence.

In the laboratory, many workers helped out on the project for which I am most grateful. Specifically, thanks to my wife Marianne, and to Ruth Jacobs for keeping things going during my absence.

On the wintering grounds, Gay (Susan G.) Simpson added considerably to the success of the field program. I appreciated the efforts of Bob Jarvis and Chuck Meslow who helped with goose collection in the spring.

My major professor, Dr. Robert L. Jarvis, contributed significantly throughout the project as advisor and co-enthusiast in the field of the ecology of waterfowl. In particular, his effort in the administrative, laboratory, data analysis (computers!) and writing aspects of the project were most welcome. Drs. C. Meslow, J. Ruben, F. Moore and F. Rickson provided critical reviews of the dissertation. My graduate school representative, Dr. E.W. Courtney, maintained an interest in the research throughout the study.

I am indebted to Maxine Avery for interpreting my handwriting and typing the first draft of the thesis. Ellen Irvine (Northwest Territories Wildlife Service) capably looked after subsequent drafts. Marc Cattet (Northwest Territories Wildlife Service) drafted the figures.

During the many years and extenuating circumstances of my project, I have received great personal support. Early discussions with David L. Trauger (U.S. Fish and Wildlife

Service) and Daniel E. Timm (Alaska Department Fish and Game) helped me clarify the direction of the research I wished to pursue. Both individuals continued their support throughout the study, including stimulating discussions with Dan throughout, followed by his prompt and constructive reviews of thesis drafts.

M.E. (Pete) Isleib, a resident Ornithologist and commercial fisherman extraordinaire, very kindly provided lodging and companionship for myself and assistants when in Cordova. True to northern legends, his open door policy set an outstanding example of hospitality. Don Shellhorn, also a resident of Cordova, made his cabin on the Copper River Delta available during field seasons there.

Gay Simpson, another co-enthusiast of waterfowl, was a true friend throughout the study. Her complete support and interesting, stimulating discussions from the beginning to the end of the project added greatly to my personal and professional development. Bob Jarvis was reliably understanding and helpful. Other fellow graduate students, Roland and Dorothy Seeger and my family in Yellowknife all supported me for the duration of my degree. Marianne's total support through the study (and amazingly, ongoing) cannot be adequately expressed.

To these people I express my sincerest thanks.

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INTRODUCTION

Studies of North American geese in the 1950's and early 1960's noted that annual variations in the average clutch sizes coincided to some extent with variation in spring phenology on nesting grounds (Cooch 1961, Barry 1962, 1966). Barry (1962) found a high degree of atresia of follicles in Atlantic Brant (*Branta bernicla hrota*) during a late spring. A key study of the condition of Canada Geese (*Branta canadensis interior*) through the reproductive season (Hanson 1962) provided direction for subsequent studies of the energetics of reproduction in geese. Studies of the energetics of Lesser Snow Geese (*Anser caerulescens caerulescens*) and Cackling Canada Geese (*B. c. minima*) have since been conducted, both during reproduction (Ankney and MacInnes 1978, Raveling 1979a) and migration (Wypkema and Ankney 1979). Considerable differences were apparent between the two species, and are expected between diverse subspecies of Canada Geese.

Several authors suggested that arctic nesting geese were largely independent of food during prelaying and egg laying periods (e.g. Ryder 1970, Ankney and MacInnes 1978, Raveling 1979a), and perhaps even until hatching (Harvey 1971). Others recorded extensive feeding before and during egg laying (e.g. Inglis 1977). Although Lack (1967) proposed that clutch size of waterfowl evolved in relation to the average availability of food for females around the time of laying, Ryder (1970) modified this for geese on the assumption that the female was totally independent of food at that time. The issue of availability and use of food by geese during the reproductive season deserves further investigation.

The flux of energy reserves prior to spring migration until arrival on the nesting grounds is poorly known. Most geese, including some races of Canada Geese, increase lipid and protein components needed on nesting grounds during migration (Hanson 1962, Barry 1966, Ryder 1967, Raveling 1979b, and Wypkema and Ankney 1979), while some geese such as Giant Canada Geese (_B_. _c_. _maxima_) apparently accumulate the major proportion of their reserves on wintering grounds prior to spring migration (McLandress and Raveling 1981). Ricklefs (1974) noted that the stages of the reproductive season are interdependent. Presumably, radically different energetic strategies during spring migration would influence strategies during all succeeding phases of the reproductive season.

Death by starvation was observed in incubating Lesser Snow Geese (Harvey 1971, and others) and Common Eiders (_Somateria mollissima_) (Milne 1963 _in_ Korschgen 1977), two species which nest in the same environment and have roughly parallel energetic strategies of reproduction (cf. Ankney and MacInnes 1978, and Korschgen 1977). Minimal body weights of the annual body weight cycle of adult female Cackling Canada Geese were also recorded near hatching (Raveling 1979a). Obviously, stress on the female goose is great, thus the opportunity to feed and availability of food are highly important. Food availability must have considerable implications in the evolution of strategies to meet the energetic demands of reproduction in northern nesting geese (see Drent and Daan [1980] for general discussion relative to all birds).

I conducted research on the energetics of migration and reproduction in female Dusky Canada Geese (_B. c. occidentalis_). Specific objectives were to: 1) document body weight and the water, protein, and lipid content of adult female geese at eight stages of migration and reproduction from premigration through hatching of eggs, 2) determine the net change and direction of change in lipid reserves and protein among six stages of reproduction, and 3) assess the contributions of food and endogenous lipid and protein to caloric requirements calculated for each period of reproduction.

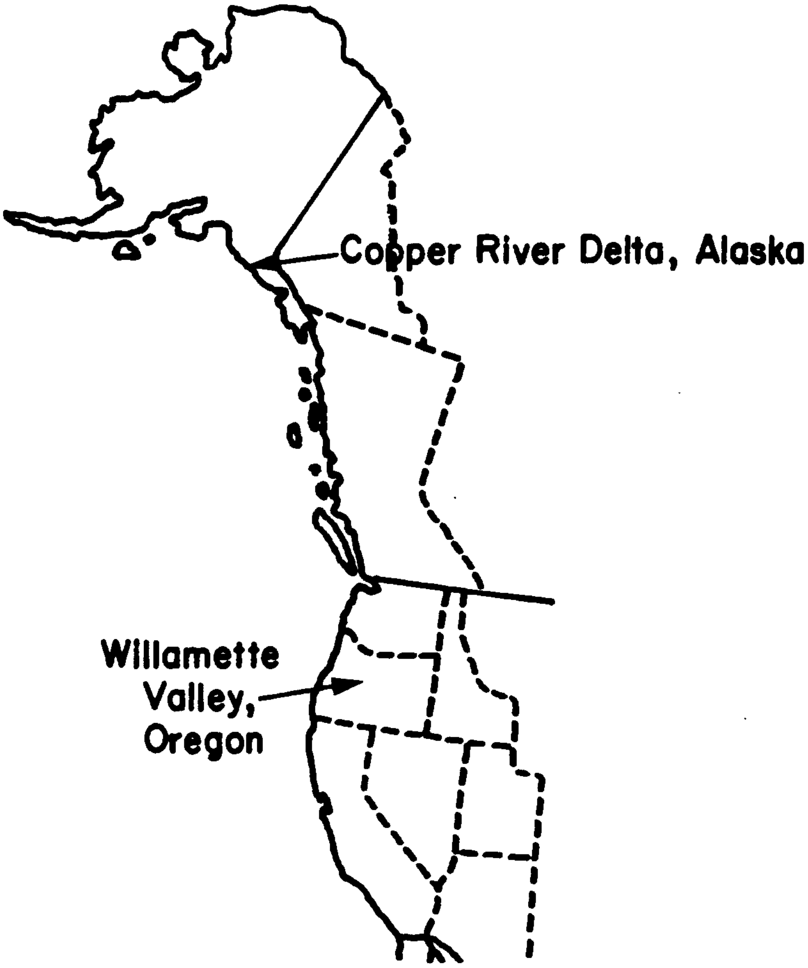
Life History

Dusky Geese winter along the lower Columbia River and in the Willamette Valley, Oregon (Pacific Flyway Waterfowl Council 1982). In late February and early March, most geese stage in large flocks on and around William L. Finley, Baskett Slough and Ankeny National Wildlife Refuges in the central Willamette Valley. Migration to the breeding grounds begins in late March and early April, and the major exodus from the refuges takes place between 8 and 14 April (Chapman et al. 1969, pers. obs.). Geese arrive on the breeding grounds on the west side of the Copper River Delta, Alaska, from early April through early May; major influxes occur between 14 and 25 April (Bromley 1976). Egg laying is initiated between late April and mid-May and is highly synchronous. Usually over 80% of the nests are initiated within an 8 to 12 day period. Clutch size is 3 to 8 eggs and incubation is 27 to 28 days (Bromley 1976, and Part II of this study). All successful eggs in a clutch usually hatch within a 24-hour period once hatching begins (pers. obs.).

Study Area

Research was conducted on the Willamette Valley National Wildlife Refuge (Willamette Valley NWR), Oregon and on the breeding grounds in Alaska. The Willamette Valley in western Oregon (Fig. 1) is dominated by small grain agriculture. Highsmith and Kimerling (1979) presented a detailed physiographic description of the region. The Willamette Valley NWR were established in the mid 1960's specifically for Canada Geese (USDI 1980). The three

Figure 1. Map of the Pacific Coast indicating the geographic location of the nesting grounds of Dusky Canada Geese (the Copper River Delta, Alaska) and the major wintering grounds in the Willamette Valley, Oregon.



refuges comprising the Willamette Valley NWR provided winter habitat for a major proportion of the Dusky Goose population during the study.

The area of study on the breeding grounds was on the west side of the Copper River Delta in south central Alaska, at approximately 60°22'N, 145°23'W (Fig. 1). The region has a history of considerable seismological activity (Reimnitz 1972), and in March 1964 an earthquake raised the Copper River Delta an average of 1.98 m. Since 1964, Crow (1968, 1972), Reimnitz (1972), and Potyondy *et al*. (1975) described the geological, hydrological and botanical changes and conditions resulting from the earthquake . Bromley (1976) compared changes in habitat use by Dusky Geese between pre-earthquake times and 1975. Plant succession continued to modify the habitat of nesting geese throughout this study.

Research was concentrated on the area (14 km^2) 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. Potyondy *et al*. (1975) described soils and vegetation on the area in 1974. The vegetational changes apparent between 1974 and 1979 were an increase in the height, density and abundance of the three major shrubs (*Alnus* spp., *Myrica gale* and *Salix* spp.) and the presence of young Sitka spruce (*Picea sitchensis*) and balsam poplar (*Populus balsamifera*).

The climate of the area is characterized by long cool winters followed by 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 this study.

METHODS

Field Procedures

Collections

Adult female geese were collected by shooting during daylight hours in 1977, 1978 and 1979. Collections were grouped according to stage of reproduction:

Premigration - within 12 days of departure from the wintering grounds.

Arrival - arrival on the breeding ground; largest ovarian follicle less than 25 mm in diameter.

Prelaying - geese with at least 1 ovarian follicle larger than 25 mm in diameter but no ovulated follicles.

Early laying - < 40% of the potential clutch laid.

Mid-laying - > 40% and < 75% of the potential clutch laid.

Late laying - > 75% of the potential clutch laid, but 1 enlarged follicle not yet ovulated.

Initiation of incubation - all enlarged follicles ovulated; 1st or 2nd day of incubation.

Hatching - from within 4 days of hatching of eggs to 1 day after hatching.

Potential clutch size was determined from examination of ovaries and counting developed and ovulated follicles (Ankney and MacInnes 1978).

In addition to stages of reproduction, 4 periods of the "reproductive season" were defined as:

Migration period - from premigration stage to arrival; 11 days.

Prelaying period - from arrival to prelaying stage; 11 days.

Laying period - from ovulation of first egg to initiation of incubation; 8 days.

Incubation period - from initiation of incubation to hatching; 27 days.

Geese were weighed within 6 hours of collection. In Oregon, specimens were frozen immediately. On the breeding grounds, geese were usually frozen within 24 hours of collection; however, some were stored under cool conditions (10°C) up to 48 hours before freezing.

Phenology

Phenology was measured on the breeding grounds by recording the timing of snow melt, reproductive activity of geese and developmental progress of certain plants characteristic of the study area. The area of snow free ground was estimated from aerial oblique 35 mm photographs taken at 3 to 4 day intervals each spring. Peak arrival (from aerial surveys and ground observations) and nest initiation dates were recorded for Dusky Geese each year. The timing of the first major Chironomid hatch on the study area was noted annually.

Laboratory Procedures

Carcass Preparation

Feathers were shaved from frozen specimens with electric sheep shears, except for rectrices and remiges which were trimmed with hand shears. The bill and feet were removed and the carcass reweighed. After partial thawing, esophageal contents were taken from the carcass and preserved for later identification. 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 still partially frozen carcass was then sectioned with a hand saw, and together with the ovary, homogenized with a meat grinder.

Determination of Carcass Composition

Triplicate 20 g subsamples were selected from the homogenate for determination of water and lipid content. Water content was assessed by drying subsamples in a forced air oven at 55°C to constant weight and calculating the difference from the original wet weight (Ricklefs 1974).

Lipid content was determined from these three subsamples by extraction using a soxhlet apparatus with a 1:1 methanol/chloroform fat solvent and an extraction period of 22 h. The solvent was replaced once after the first 11 h. Nitrogen was measured from duplicate 5 g subsamples using the Kjeldahl method, and converted to crude protein by multiplying by a conversion factor of 6.25 (Horowitz 1970: 16, 127).

Body weight refers to the weight of the entire goose at the time of collection. The terms carcass and carcass components are used here in reference to weight of the goose after removal of feathers, bill, feet, and esophageal contents. Carcass components are reported as absolute values (g) and as percentages of the carcass weight.

Energy reserves were defined as the caloric yield from oxidation of lipid and protein not required for the basic structure of the living goose. I assumed that the amounts of structurally required lipid and protein were those average amounts remaining in adult female geese at the hatching stage when those components were at minimum levels for the reproductive season. Raveling (1979a) noted that during the annual cycle the protein content was lowest in adult female Cackling Canada Geese at hatching and that lipids remaining were probably structural. Energy yields of 9 kcal/g lipid and 4.3 kcal/g protein were used in calculation of caloric yield from catabolism of energy reserves as recommended by Ricklefs (1974).

Calculation of Daily Energy Expenditure

The use of metabolic rate equations and multiples thereof in estimating daily energy requirements of free-living birds was reviewed by Raveling (1979b). The equation used here for basal metabolic rate was BMR in kcal/day = $73.5\ W^{0.734}$; W = body weight in kg (Aschoff and Pohl 1970). Energy used during migratory flight was estimated as 12 times BMR, as suggested by Raveling and LeFebvre (1967). For the remainder of the migration period, and for the prelaying and laying periods, energy expenditure was estimated at 3.4 BMR (King 1973). Daily energy requirements during incubation were estimated at 1.25 BMR (Aschoff and Pohl 1970, King 1973). When energy reserves increased during a period, the cost of protein and lipid synthesis was added to the metabolic requirements for the period (see Raveling 1979b). This cost was the energy content of the tissue (5.65 kcal/g protein, 9.45 kcal/g lipid) (Ricklefs 1974) plus the cost of conversion at 70% efficiency (1.43 x energy content) (King 1973). Conversion efficiency as used here does not include specific dynamic action or digestive efficiency; these are included in the metabolic rate equations for the different periods. The daily energy costs of transporting and converting endogenous lipids and protein into a clutch of eggs were estimated as in Raveling (1979b) with one exception. The time required for formation of the clutch was extended to 20 days (12 days for formation of 5.6 eggs [Grau 1976], 8 days for laying of the clutch), as Dusky Geese laid eggs at a rate of 1 egg/1.5 days. The daily cost of egg formation was then added to daily requirements during the prelaying and laying periods.

Protein content calculated as above for an average clutch of eggs was more than the average amount of protein lost from goose carcasses during the egg laying period. Thus, the caloric 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 calculated as the caloric yield of the net negative change in energy reserves averaged over the number of days in a period. The remaining energy not accounted for by energy reserves was assumed to be provided from food sources. When the net change in energy reserves was positive, all energy requirements were assumed to be supplied from metabolism of food.

Statistical Analysis

Statistical procedures followed Nie *et al*. (1975) and Tuccy (1980) unless otherwise noted. A probability level of 0.05 was set as the minimum required for significance. Two-way analysis of variance (*ANOVA*) was used to investigate differences in body weight, energy reserves and measures of carcass composition over 5 stages of reproduction (premigration, arrival, prelaying and initiation of laying merged into one stage, initiation of incubation and hatching). Relationships between carcass components and clutch size were investigated using linear regression. To compare components with potential clutch size, geese from the prelaying and initiation of laying stages were combined into one sample; whereas for regressions with number of eggs laid, all specimens from prelaying collections through initiation of incubation were combined into one group.

Terminology

The concept of "protein reserves" and the expression itself, is not widely accepted in zoological literature (Allison 1959, Wannemacher and Cooper 1970), despite its wide use in animal science (Agricultural, e.g., Swick and Benevenga 1977) and recent ornithological literature (e.g., Jones and Ward 1976, Ankney and MacInnes 1978, Fogden and Fogden 1979, Raveling 1979a, and others). Some of the authors refer to "protein stores", an expression which implies a depot of secluded, non-functional protein similar to fat depots. All endogenous protein is dynamic, demonstrating constant turnover (Kreutler 1980) and cannot accurately be considered in this way. In order to be consistent with the most applicable body of literature, I have retained the term "protein reserves" and accept the definition cited in Wannemacher and Cooper (1970:122) for the purposes of this report. Their definition reads:

> "...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."

A detailed review of the terminology used in literature addressing the energetics of animals, particularly the class Aves, is needed.

RESULTS

Phenology and Collections

The three years of the study were exceptionally early on the nesting grounds (Table 1). Winter weather on the Copper River Delta was mild, with little snow and ice accumulation and generally above freezing temperatures. Snow melt was complete in April of each year (Table 2). Prostrate willow (*Salix arctica*), sedges (*Carex* spp.), horsetail (*Equisetum* spp.) and forbs on the study area responded with early emergence of leaves and shoots. Measures of phenology and reproductive activity of geese were similar each year (Table 2), as were dates of collections of geese keyed to reproductive events (Table 3). Food was 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. During all years of the study, geese began laying eggs earlier than previously recorded for the population (Trainer 1959, Timm 1973, Bromley 1976). Clutch size averaged 5.6 eggs (n=650) each year of the study and eggs weighed during laying and early incubation averaged 144 g (1977 - 140 g, n=30, s.d. = 8.3; 1978 - 144 g, n = 156, s.d. = 9.5; 1979 - 145 g, n = 188, s.d. = 11.7).

Table 1. Summary of weather parameters from 20 April through 30 June 1977-1979 for the Copper River Delta, Alaska.[a]

Parameter	April[b]	May	June
Mean minimum temperature (°C)	-0.4	2.9	6.0
Mean maximum temperature (°C)	9.9	11.6	13.4
Precipitation (cm)	3.8	12.1	15.4
Wind speed (km/h)	4.0	4.6	3.2

[a] From USDC 1977-1979

[b] Last 10 days of April, when geese were present

Table 2. Dates of occurrence of selected phenological events on the Copper River Delta, Alaska.

Phenological event	Timing		
	1977	1978	1979
Study area snow free	22 April	Prior to 14 April	25 April
Peak of *Iris setosa* flowering	29 June	28 June	26 June
Peak of *Dodecatheon pulchellum* flowering	1 June	1 June	15 June
First major Chironomid hatch	10 May	5 May	5 May
Major arrival of geese	17-22 April	14-20 April	18-25 April
Date of first nest initiation (geese)	29 April	22 April	29 April
Peak of nest initiation (geese)	4-5 May	6-7 May	4-5 May

Table 3. Number of adult female Dusky Canada Geese collected by date and stage of reproduction.

	1977		1978		1979		
Stage	N	Dates	N	Dates	N	Dates	Total
Premigration	6	4-13 April	14	3-13 April	16	5-13 April	36
Arrival	16	15-21 April	12	16-20 April	15	16-22 April	43
Prelaying	1	3 May	2	5-6 May	5	29 April-5 May	8
Early laying	6	4-8 May	8	4-13 May	4	30 April-8 May	18
Mid-laying	2	5-7 May	1	13 May	3	6-7 May	6
Late laying	2	7-8 May	0	---	2	6-7 May	4
Initiation of incubation	3	7-8 May	0	---	5	7-16 May	8
Hatching	15	5-15 June	14	7-15 June	10	7-12 June	39
Total	51		51		60		162

Annual Measures of Body Weight and Carcass Components

In a series of 2-way ANOVA (reproductive stage and year), body weight, carcass components and caloric yield of energy reserves (Table 4) were significantly different at each reproductive stage and reproductive stage accounted for the most variation in each component (Table 5). Significant differences between years were indicated for grams of protein and proportion of protein, although relatively little variance was accounted for by year. Significant interactions between stage of reproduction and year occurred with 5 of the variables measured (Table 5), but the ms_{Av}/ms_{AL} statistic (Linquist 1953) indicated that the rank order of effectiveness of the stages was approximately the same within years for all 5 variables, even though their relative effectiveness differed from year to year. Because the general patterns of change for all components were the same each year, because differences between stages were the major focus of interest, and because variation accounted for by year was relatively small, I pooled all measures over years at each stage for further analysis (Table 6).

Body Weight

Mean body weight varied from a high of 3627 g during initiation of egg laying to 2495 g at hatching (Table 6, Fig. 2), a loss of 31.3% of initial body weight during about

Table 4. Mean body weight and composition of adult female Dusky Canada Geese on the Copper River Delta, Alaska, by stage of reproduction and year. Standard error (or range when $n \leq 3$) in parenthesis.

Component	Year	Pre-migration	Arrival	Pre-laying	Initiation of laying	Mid-laying	Late laying	Initiation of incubation	Hatching
Body weight (g)	1977	3547(137)	3245 (66)	3358 --	3558(183)	3425(3041-3808)	3473(3227-3719)	3428(3358-3469)	2569(41)
	1978	3556(59)	3009(88)	3602(3348-3855)	3620(81)	3076 --	-- --	-- --	2436(51)
	1979	3460(77)	3115(62)	3666(106)	3744(116)	3739(3640-3842)	3289(3205-3373)	3072(53)	2467(69)
Lipid (g)	1977	963(29)	531(35)	519 --	530(58)	361(167-554)	556(509-603)	554(513-593)	77(11)
	1978	1050(40)	440(46)	496(281-710)	494(27)	302 --	-- --	-- --	59(9)
	1979	900(50)	504(27)	627(48)	577(38)	538(464-590)	457(435-479)	388(34)	48(5)
Protein (g)	1977	562(22)	565(11)	576 --	628(35)	595(511-679)	566(532-601)	576(564-589)	504(11)
	1978	521(11)	531(15)	629(581-676)	618(17)	513 --	-- --	-- --	463(10)
	1979	518(9)	488(13)	608(27)	595(22)	567(541-605)	479(464-493)	522(21)	436(15)
Water (g)	1977	1694(74)	1798(33)	1917 --	1970(96)	1823(1676-1970)	1857(1754-1959)	1857(1715-1984)	1629(26)
	1978	1625(30)	1704(34)	1994(1961-2027)	2009(65)	1801 --	-- --	-- --	1577(34)
	1979	1625(39)	1711(34)	2018(36)	1950(53)	2035(1982-2134)	1841(1823-1860)	1750(30)	1591(56)

Table 4 continued

Component	Year	Pre-migration	Arrival	Pre-laying	Initiation of laying	Mid-laying	Late laying	Initiation of incubation	Hatching
Lipid (%)	1977	29.5(1.0)	17.8(1.0)	16.6 --	16.0(1.5)	11.0(5.9-16.1)	18.4(18.1-18.7)	18.2(16.3-20.0)	3.3(0.4)
	1978	31.8(1.0)	15.6(1.2)	14.0(8.6-19.4)	14.5(0.6)	10.7 --	-- --	-- --	2.6(0.4)
	1979	28.1(1.2)	17.6(0.7)	18.2(0.9)	16.7(1.6)	15.6(14.2-16.4)	15.4(14.7-16.1)	14.0(1.1)	2.1(0.2)
Protein (%)	1977	17.2(0.4)	19.1(0.3)	18.6 --	19.8(0.3)	20.0(19.5-20.4)	18.6(18.4-18.7)	18.8(18.6-19.0)	21.7(0.3)
	1978	15.8(0.3)	19.2(0.3)	19.4(19.0-19.8)	19.1(0.2)	18.9 --	-- --	-- --	20.9(0.3)
	1979	16.4(0.4)	17.1(0.4)	18.0(0.7)	18.1(0.6)	17.0 --	16.2 --	18.9(0.9)	19.5(0.5)
Water (%)	1977	51.6(0.6)	60.8(0.7)	61.9 --	61.6(0.7)	61.1(58.5-63.6)	60.4(59.6-61.3)	60.3(57.8-62.4)	70.0(0.5)
	1978	49.3(0.5)	61.9(0.8)	61.8(56.9-66.7)	61.8(0.5)	66.5 --	-- --	-- --	70.9(0.4)
	1979	51.2(0.8)	60.0(0.6)	59.9(0.7)	59.2(0.6)	61.0(60.3-62.1)	62.3(61.2-63.4)	63.2(0.5)	70.9(0.7)
Reserve calories[a] (kcal)	1977	8489(301)	4608(330)	4549 --	4879(631)	3206(1107-5305)	4844(4270-5417)	4871(4558-5162)	260(112)
	1978	9093(376)	3641(458)	4567(2431-6702)	4502(303)	2329 --	-- --	-- --	-72(96)
	1979	7728(454)	4040(2610)	5663(489)	5152(299)	4682(3907-5101)	3578(3443-3713)	3137(232)	-288(93)

[a] Total reserve calories were calculated as the caloric yield of body tissues above the average content at hatching (2597 kcal) from all years combined (see text).

Table 5. Effects of stage of reproduction and year of collection on body weight and carcass components of adult female Dusky Canada Geese.

Component	Stage[a] ETA[b] (significance of F)	Year[c] ETA (significance of F)	Significance of interaction	MS_{AV}/MS_{AL}[d]
Body weight (g)	0.86 (0.001)	---	---	---
Lipid (g)	0.67 (0.001)	0.26 (0.001)	---	---
Protein (g)	0.93 (0.001)	---	0.007	---
Water (g)	0.71 (0.001)	---	---	---
Lipid (%)	0.95 (0.001)	---	0.007	149.0
Protein (%)	0.76 (0.001)	0.42 (0.001)	0.005	22.5
Water (%)	0.95 (0.001)	---	0.015	241.0

[a] Stages of reproduction were: premigration, arrival, prelaying/initiation of laying, and hatching.

[b] ETA is a measure of association which can vary from 0 (means are identical) to a maximum value of 1 (means are very different and the variances within the independent variable are small).

[c] Year = 1977, 1978, 1979.

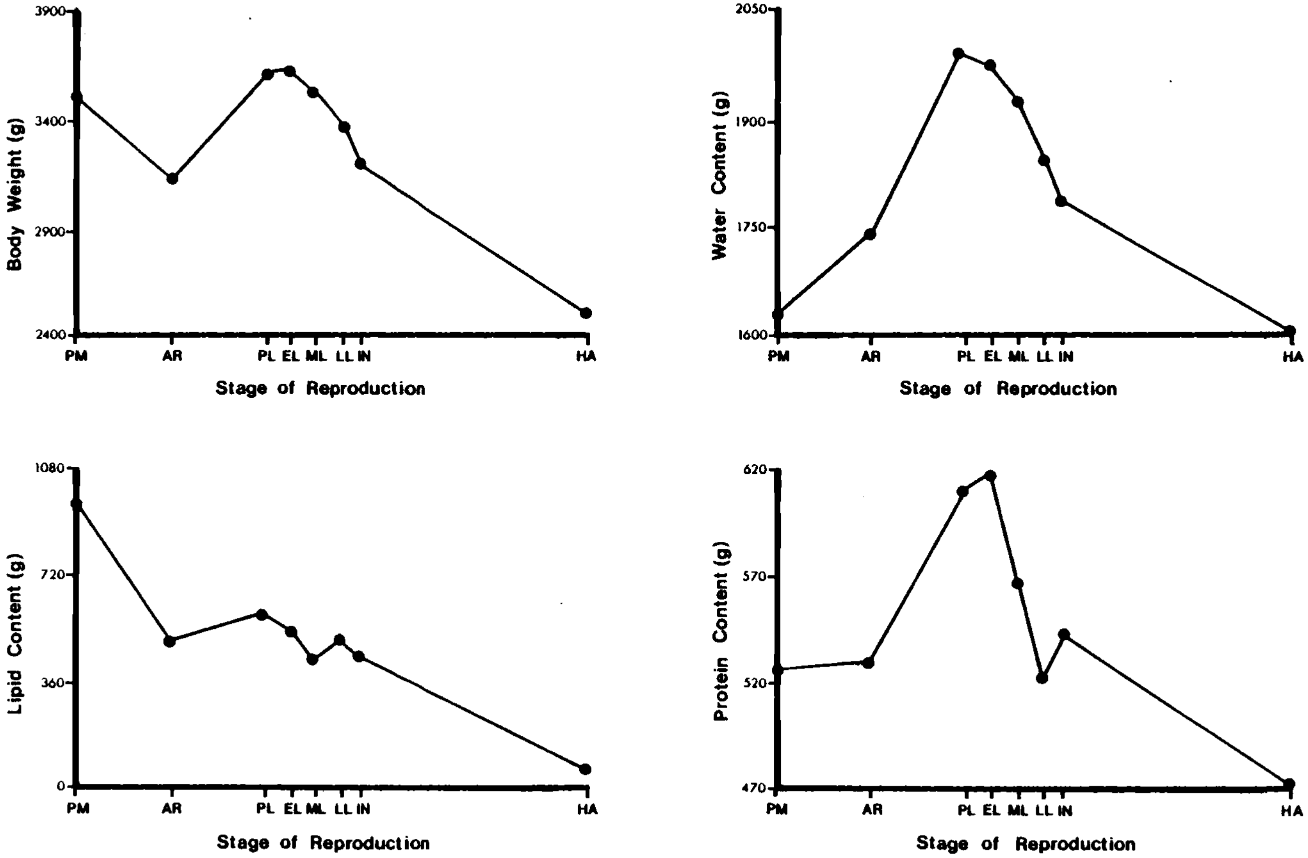
[d] Ratio > 12 indicates rank order of effectiveness of the stages is approximately the same within years (Lindquist 1953).

Table 6. Mean (and standard error) body weight and composition of adult female Dusky Canada Geese by stage of reproduction, 1977-1979. For sample sizes see Table 3.

Component	Pre-migration	Arrival	Pre-laying	Early laying	Mid-laying	Late laying	Initiation of incubation	Hatching
Body weight (g)	3512(46)	3134(43)	3612(88)	3627(78)	3524(150)	3381(119)	3206(73)	2495(30)
Lipid (g)	969(29)	496(21)	581(55)	524(24)	439(69)	507(36)	450(37)	63(6)
Protein (g)	527(7)	529(9)	609(19)	616(14)	567(26)	523(30)	543(16)	472(8)
Water (g)	1637(24)	1741(20)	1999(25)	1983(43)	1926(66)	1849(43)	1790(37)	1601(21)
Lipid (%)	29.8(0.7)	17.1(0.6)	17.0(1.3)	15.5(0.7)	13.2(1.7)	16.9(0.9)	15.6(1.1)	2.8(0.2)
Protein (%)	16.3(0.2)	18.5(0.2)	18.4(0.5)	19.1(0.2)	18.3(0.7)	17.4(0.8)	18.9(0.6)	20.8(0.3)
Water (%)	50.5(0.4)	60.8(0.4)	60.6(1.1)	61.2(0.4)	61.9(1.1)	61.4(0.8)	62.1(0.8)	70.6(0.3)
Reserve calories (kcal)	8386(270)	4140(203)	5250(538)	4772(251)	3798(705)	4211(438)	3787(351)	0(69)

Figure 2. Graphic representation of the chronology of body weight and carcass components at premigration (PM), arrival on the nesting grounds (AR), prelaying (PL), early laying (EL), mid-laying (ML), late laying (LL), initiation of incubation (IN), and hatching (HA).

Figure 2.


3900
3400
2900
2400
Body Weight (g)
PM
AR
PL
EL
ML
LL
IN
HA
Stage of Reproduction
2050
1900
1750
1600
Water Content (g)
PM
AR
PL
EL
ML
LL
IN
HA
Stage of Reproduction
1080
720
360
0
Lipid Content (g)
PM
AR
PL
EL
ML
LL
IN
HA
Stage of Reproduction
620
570
520
470
Protein Content (g)
PM
AR
PL
EL
ML
LL
IN
HA
Stage of Reproduction

34 days. Weight loss during migration was entirely due to catabolism of lipids (Table 6). The ensuing gain of weight through initiation of egg laying was accounted for by increases in all components. Body weight declined rapidly thereafter through egg laying and incubation as water, protein and particularly lipid components decreased. Analysis of variance for body weight over 5 stages indicated significant differences between each stage through the reproductive season (Table 7).

Water

Water was the major carcass component, accounting for 50.5 to 70.6% of the carcass weight (Fig. 3). Water content increased 362 g during the migration and the prelaying periods to a peak of 1999 g (Table 6, Fig. 2). By hatching, carcasses contained an average of 1601 g of water. Water content changed significantly between each of the 5 stages tested (Table 7). As a proportion of the carcass, water increased significantly during migration, changed little during prelaying and laying stages, and increased significantly again during incubation (Table 6, Fig. 2).

Protein

Protein content did not change during migration but increased 80 g during the prelaying period (Table 6). A

Table 7. Analysis of the significance of changes in body weight and carcass components of adult female Dusky Canada Geese between selected stages of reproduction.

	Stage of Reproduction													
	Premigration (n=36)			Arrival (n=43)			Prelaying/laying[a] (n=26)			Initiation of Incubation (n=8)			Hatching (n=39)	
Parameter	$\bar{x}$	SE	P[b]	$\bar{x}$	SE	P	$\bar{x}$	SE	P	$\bar{x}$	SE	P	$\bar{x}$	SE
Body weight (g)	3512	46	**	3134	43	**	3622	60	**	3206	73	**	2495	30
Lipid (g)	969	29	**	496	21	NS	542	24	*	450	37	**	63	6
Protein (g)	527	7	NS	529	9	**	614	11	**	543	16	**	472	8
Water (g)	1637	24	*	1741	20	**	1988	30	**	1790	37	**	1601	21
Lipid (%)	29.8	0.7	**	17.1	0.6	NS	16.0	0.6	NS	15.6	1.1	**	2.8	0.2
Protein (%)	16.3	0.2	**	18.5	0.2	NS	18.9	1.1	NS	18.9	0.6	**	20.8	0.3
Water (%)	50.5	0.4	**	60.8	0.4	NS	61.0	0.4	NS	62.1	0.8	**	70.6	0.3
Reserve calories (kcal)	8386	270	**	4140	203	*	4919	238	*	3787	351	**	0	69

---

[a] Prelaying geese and geese initiating egg laying were lumped as one stage for this analysis.

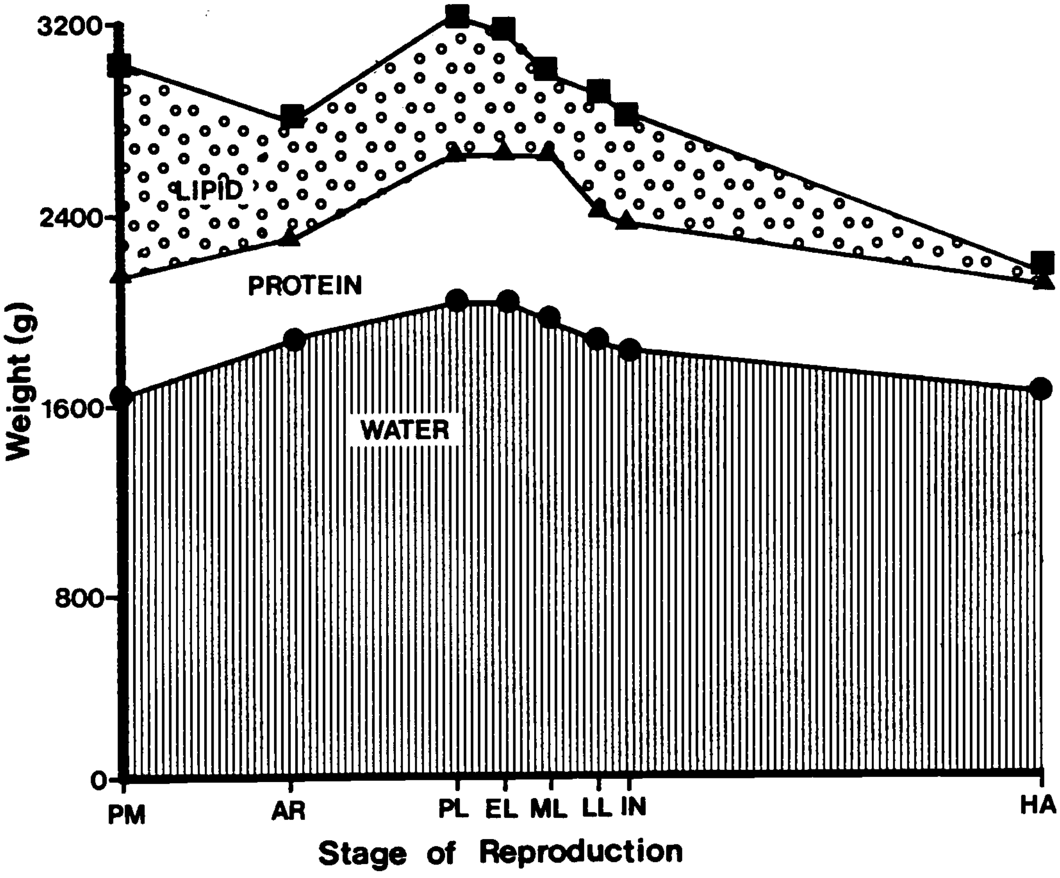
[b] P is the probability from one-way analysis of variance that means in adjacent columns are different by chance.

** $P<0.05$

* $0.05<P<0.10$

Figure 3. Cumulative weight of components for adult female Dusky Canada Goose carcasses collected during 8 stages of reproduction.

Figure 3


3200
2400
1600
800
0
Weight (g)
LIPID
PROTEIN
WATER
PM
AR
PL
EL
ML
LL
IN
HA
Stage of Reproduction

decline of 86 g between the prelaying and late laying stages was followed by an increase of 20 g as laying was completed and incubation initiated; a net loss of 66 g occurred during the laying period. A decrease of 71 g occurred during incubation. Significant changes occurred between the last 4 stages of the 5 tested (Table 7). The proportion of protein in the carcass ranged from 16.3% at premigration to 20.8% at hatching, and had the least variation of the three components (Fig. 3). Significant changes occurred however, between premigration and arrival, and between initiation of incubation and hatching (Table 7).

Lipids

During migration lipid content of geese decreased 473 g from a peak of 969 g at premigration (Fig. 2). This loss was only partially recovered during the prelaying period when 85 g of lipids were added to reserves. Lipids decreased through mid-laying to 439 g, then partially recovered to 507 g by late laying. A considerable decrease of 444 g was recorded during late egg laying and incubation. Significant decreases in grams of lipids were observed between premigration and arrival, and between initiation of incubation and hatching (Table 7). The dynamics of the proportion of the carcass composed of lipids generally paralleled the changes in the absolute amounts of lipids (Fig. 3), with significant changes between the same stages as seen with grams of lipids (Table 7). A decrease in the amount of lipids approached significance between prelaying/initiation of laying and initiation of incubation ($0.05 < p < 0.10$); this decrease was believed to be biologically significant.

Energy Reserves

Lipids accounted for the major proportion of energy reserves (i.e. lipids above 63 g, see Methods) at all stages measured throughout the reproductive season (Fig. 4), except at hatching where I assumed all reserves had been depleted. Protein reserves (i.e. those amounts above 472 g) peaked during prelaying and early laying, then decreased through incubation (Fig. 2), but never represented more than 13.1% of the potential caloric yield of energy reserves.

Energy reserves declined continuously during the reproductive season, except during the prelaying period when geese actually increased reserves 1109 kcal (Fig. 4). Lipids and protein accounted for 765 kcal and 344 kcal, respectively, of the increase in caloric reserves measured during prelaying. Migration was the most costly period, followed by incubation and laying (Table 8). For the 5 stages examined, energy reserves decreased significantly between premigration and arrival, and between initiation of incubation and hatching (Table 7). The increase in energy reserves between arrival and prelaying/initiation of laying

Figure 4. Energy (kcal) accounted for by protein reserves and lipid reserves for adult female Dusky Canada Geese at different stages of reproduction.

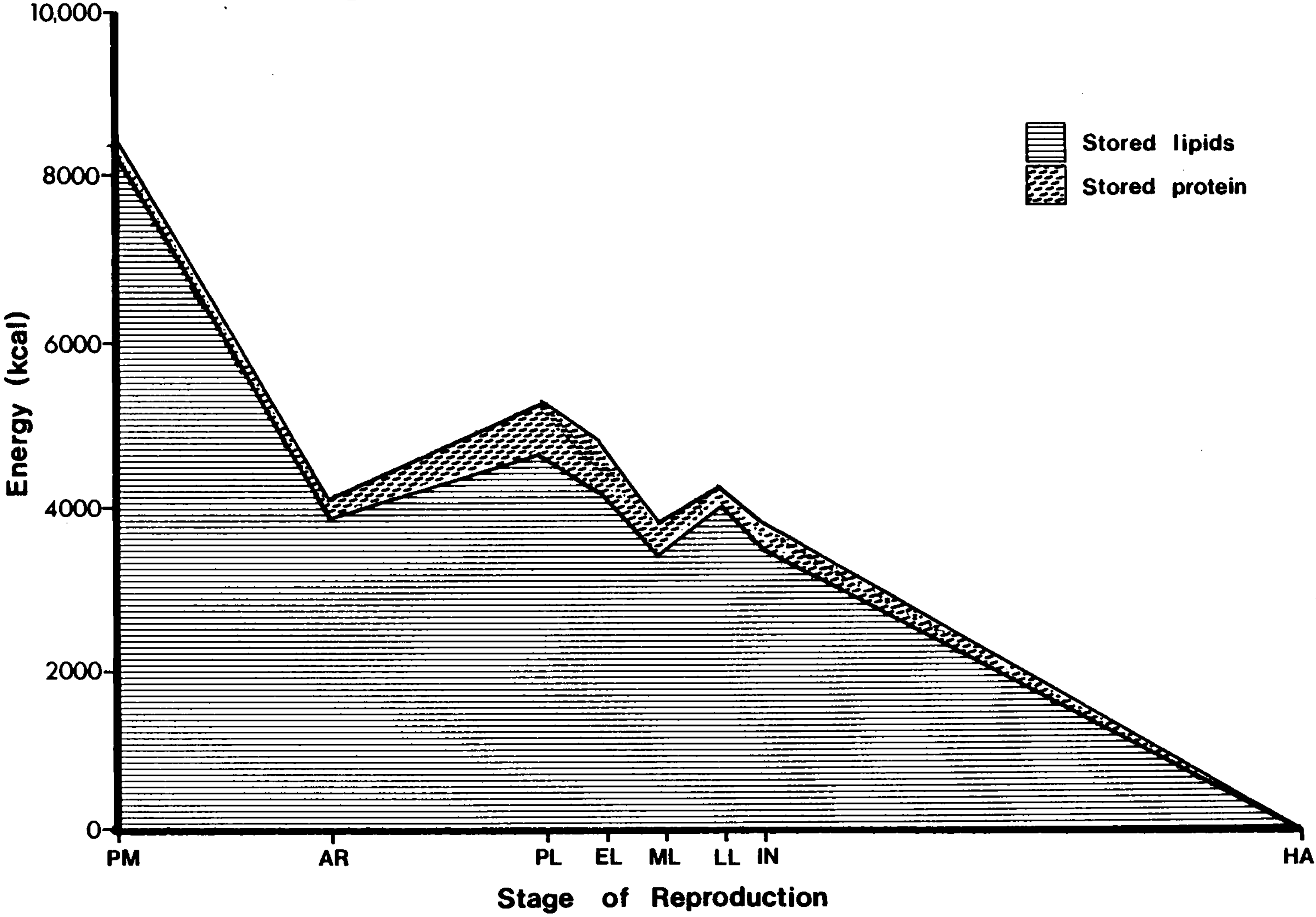


Table 8. Net change in energy reserves of adult female Dusky Canada Geese during four periods of reproduction.

Period of reproduction	Lipid			Protein			Total caloric reserves	
	% change	g	Caloric yield	% change	g	Caloric yield	% change of reserves	Changes in kcal
Migration	-52.2	-473	4257	+3.6	+2	9	-51.1	-4248
Prelaying	+19.6	+85	765	+140.0	+80	344	+26.8	+1109
Egg laying	-25.3	-131	1179	-48.2	-66	284	-27.9	-1463
Incubation	-100.0	-387	3483	-100.0	-71	305	-100.0	-3788

and the decrease between prelaying/initiation of laying and initiation of incubation, although not statistically significant ($0.05 < \underline{p} < 0.10$), were believed to be biologically significant (Table 7).

Maturation of Follicles

Geese began the period of rapid maturation of follicles about the time of their arrival on the nesting grounds or shortly thereafter. Assuming this period is 13 days (Grau 1976) and the peak of nest initiation occurred between 4 and 7 May each year, peak numbers of arriving geese should have been observed on or before 21 to 24 April. In fact, this was the case (Table 2).

Further evidence of the timing of rapid maturation of follicles was observed in the size of the largest follicle in geese collected during the arrival stage on the delta. The average size of the largest follicle measured in 30 geese collected between 15 and 21 April (Table 9) indicated a slow rate of growth ($\bar{x} < 0.09$ mm/day) until 20 April when a growth rate greater than 2 mm/day was determined. 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 9), a follicle of 42.3 mm diameter would be expected by 3 May. This projection was consistent with a follicle diameter between 43 and 44 mm typical of Dusky Geese at

Table 9. Average largest follicle size for 30 Dusky Canada Geese collected on the Copper River Delta, Alaska, 1977-1979.

Date	$\bar{x}$ 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.

ovulation (Bromley unpubl. data) and with the peak of laying dates of 4 to 7 May observed during the 3 years.

Relationship of Carcass Composition to Number of Eggs Laid

Correlation analysis of the weights and proportions of carcass components in prelaying geese and those initiating egg laying with the potential clutch size of the birds (Table 10) revealed no relationship between the two factors. Potential clutch of collected geese averaged 5.6 eggs (n = 13, s.d. = 0.8), 5.4 eggs (n = 10, s.d. = 0.7) and 6.2 eggs (n = 13, s.d. = 1.2) in 1977, 1978, and 1979 respectively. The regression of body weight and amounts of carcass components against the number of eggs laid for laying geese, however, indicated a definite drain on reserves as laying progressed (Table 10). This relationship was most strongly indicated for grams of protein (r = -0.56) which declined as eggs were laid. Similar relationships were evident for water (r = -0.51), lipid (r = -0.40) and energy reserves (r = -0.47). Of the proportionate measures of carcass composition, only percent water was significantly correlated with number of eggs laid (r = -0.28). Thus, the number of eggs laid appeared to be related to the weights of stored reserves and water, rather than to proportionate amounts of the carcass components.

Table 10. Correlation of body weight and carcass components with number of eggs laid by adult female Dusky Canada Geese[a] (n=39) and with potential clutch size of geese (n=22).

	With number of eggs laid		With potential clutch size	
Component	r	significance of r	r	significance of r
Body weight (g)	-0.53	0.01	-0.03	NS
Lipid (g)	-0.40	0.01	-0.31	NS
Protein (g)	-0.56	0.01	-0.21	NS
Water (g)	-0.51	0.01	-0.13	NS
Lipid (%)	-0.17	NS	-0.28	NS
Protein (%)	-0.14	NS	-0.04	NS
Water (%)	0.28	0.05	0.17	NS
Reserve calories (kcal)	-0.47	0.01	-0.28	NS

[a] Geese collected (1) during prelaying, laying and initiation of incubation stages were grouped for correlation with eggs laid and (2) during prelaying and initiation of egg laying for correlation with potential clutch size.

Role of Endogenous Reserves and Food in Meeting the Daily Energy Requirements

Energy expenditure calculated for each period of reproduction ranged from 198 kcal/day during incubation to 843 kcal/day during migration (Table 11). If the energy content of eggs being laid is included, energy requirements peaked during egg laying at 856 kcal/day. Assuming calculations of energy supplied by combustion of stored energy reserves were correct, and remaining energy needs were derived from food, caloric requirements during migration were met almost equally by catabolism of lipid reserves and by food intake. During prelaying and laying periods, food provided almost all of the energy needs of geese, although energy reserves utilized during laying were similar to the energy content of an average clutch of eggs (Table 11). Energy reserves played a major role in meeting energy requirements of the incubation period.

The net change in energy reserves during each of the 4 periods of reproduction illustrated the relative importance of stored energy to each period (Table 8). The largest amount of reserves was expended during migration, and the second largest amount during the incubation period. Geese added to reserves during prelaying, while expending slightly more during laying than was stored the previous period. Relative to the contribution of energy from food, energy reserves were most important during the incubation period,

Table 11. Contribution of energy reserves and food to daily energy requirements of adult female Dusky Canada Geese during four periods of reproduction.

Reproductive period	Number of days	Body weight (kg)		Daily energy needs (kcal)[a]	Net contribution from reserves				Contribution from food	
		Range	Midpoint		Lipid (g)	Protein (g)	Caloric yield (kcal)	% of daily needs	kcal	% of daily needs
Migration	11	3.51-3.13	3.32	843	43.0	0	387	45.9	456	54.1
Prelaying	11	3.13-3.61	3.37	793	0	0	0	0	793	100.0
Egg laying excluding 5.6 eggs	8	3.61-3.21	3.41	689	3.8	9	36	5.2	653	94.8
including 5.6 eggs	8	3.61-3.21	3.41	856	16.5	6.7	192	22.4	665	77.6
Incubation	27	3.21-2.49	2.85	198	14.3	2.6	131	66.1	67	33.9

[a] Daily energy requirements were calculated as: migration 12BMR for 40 h, 3.4 BMR remainder of migration; prelaying, 3.4 BMR; egg laying, 3.4 BMR; incubation, 1.25 BMR (see Part I Methods).

[b] Food was assumed to provide that part of a goose's daily energy requirements not accounted for by a loss in stored energy reserves.

followed by the migration and laying periods. Energy reserves did not contribute to energy requirements during the prelaying periods.

Reserves accumulated on the wintering grounds were important throughout the reproductive season (except during prelaying) while those derived on the nesting grounds were utilized during egg laying and incubation (Table 12).

Table 12. Partitioning of reserves accumulated on wintering and nesting grounds over four periods of reproduction. Numbers in parentheses are percentages.

Source of component	Accumulated reserves	Reserves utilized during			
		Migration	Prelaying	Egg laying	Incubation
<u>Lipids</u> (g)					
Wintering	906 (91)	473 (100)	0	46 (35)	387 (100)
Nesting	85 (9)	0	0	85 (65)	0
Total	991 (100)	473 (100)	0	131 (100)	387 (100)
<u>Protein</u> (g)					
Wintering	55 (41)	0	0	0 (0)	55 (77)
Nesting	80 (59)	0	0	66 (100)	14 (20)
Total	135 (100)	0	0	66 (100)	69 (97[a])
<u>Energy</u> (kcal)					
Wintering	8386 (88)	4246 (100)	0	414 (28)	3787 (8)
Nesting	1109 (12)	0	0	1049 (72)	60 (2)
Total	9495 (100)	4246 (100)	0	1463 (100)	3847 (100)

[a] Protein content increased 2 g during the migration period, thus cannot be assigned to the wintering or nesting grounds.

DISCUSSION

Treatment of Data

Pooling data over the 3 years of the study may have introduced some error into analysis, but I suggest any errors were minimal. The 3 years were very similar phenologically and hence, influence of weather on weights and carcass composition should have been minor. In addition, year accounted for only a minor amount of variation as compared to reproductive stage, in a 2-way ANOVA. Thus, pooling of data for the 3 years was justified. Errors may have also occurred from small sample sizes at some stages of reproduction. Individual variation in carcass components and body weight of geese at identical stages of reproduction was often considerable, as revealed by relatively high standard errors (Table 6). Much of the variation was possibly attributable to variation in body size, but the correlation analysis of several morphological measurements with body weight and carcass components revealed no consistently reliable index of body size (unpubl. data). Despite the large variability in many of the parameters measured, differences between stages of reproduction were often significant. Thus, I believe that dynamics of components were accurately described.

In discussing reserves versus protein and lipids derived from food, the dynamic nature of the reserves must be kept in mind. There is continual anabolism and catabolism of reserves (Allison 1959); for example, protein is discussed below as one component of carcasses, but protein itself consists of many constituent amino acids each of which may play important and unique roles at different stages of the life cycle (e.g. Allison 1959, Fisher 1967, Scott 1973). Thus, when it is stated, for example, that lipids in eggs were derived largely from food lipids it is meant that a net amount of lipids rather than the specific lipids ingested by the birds were utilized in egg formation.

Migration

Lipid content of adult female Dusky Geese reached a peak for the entire reproductive season just before spring migration. Although not measured during migration, the considerable drain (473 g) on lipid stores during the brief spring migration suggested that the premigration peak was probably supplemented little, if at all, during migration. Fat content of premigration female Dusky Geese (29.8%) was similar to measurements of female Giant Canada Geese (29.0%, McLandress and Raveling 1978), while protein (Dusky 16.3%, Giant 18.1%) and water (Dusky 50.5%, Giant 44.7%) differed only slightly. In contrast to those subspecies, Cackling Canada Geese and Interior Canada Geese gained little or no weight before migration (Raveling and Lumsden 1977, Raveling 1979a).

Dusky Geese depleted their lipid reserves by more than half during migration. The Giant Canada Goose, which has a short migration (885 km, McLandress and Raveling 1978) possibly experienced little loss of lipid stores during migration, as Raveling (1979a) reported "prelaying" (collected between arrival and egg laying) adult females (unknown sample size) contained 29.1% fat, almost identical to the 29% fat of premigration Giant Canada Geese reported by McLandress and Raveling (1981). Brant, Lesser Snow Geese, White-fronted Geese, Ross' Geese, and Cackling and Interior Canada Geese all experienced weight gains during spring migration, and arrived on nesting grounds at near peak body weights (Barry 1966, Ankney and MacInnes 1978, Raveling and Lumsden 1977, Raveling 1979a). Thus, the chronology of energy reserves in Dusky Canada Geese was unique among geese studied to date, in that the cost of migration in energy reserves was the most severe of all periods in the reproductive season. This finding was in contrast to a statement supported by Raveling and Lumsden (1977:49) 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".

The migration route of Dusky Geese is about 2,600 km long and lies largely along coastal Washington, British Columbia and Alaska. Because of the maritime climate, geese are able to migrate quickly, without awaiting the 32°F (0°C) isoclines as do some geese in the interior of the continent (Ryder 1967, Cooper 1978). (One observation of a family group of 5 Dusky Geese including 3 neck-collared individuals, revealed migration from Oregon to the breeding grounds in 4 days, although an average time for migration based on mass emigration from the refuges and major influxes on the nesting grounds was about 11 days.) The terrain enroute is typically fiord-like and offers little to migrating geese in the way of extensive staging areas with high quality forage (see Isleib 1979, Pitelka 1979). Where appropriate habitat occurs, it is used by a resident breeding population of Vancouver Canada Geese (_B. c. fulva_) and other migrating geese. The possibility for competition on those areas in spring therefore exists. Thus, Dusky Geese probably stage little during migration, but rather complete migration quickly.

Based on the characteristics of the Dusky Goose spring migration, I suggest that the cost of migration to energy reserves and the influence of this cost on the overall energetic strategy of reproduction evolved by geese can be significant, and is related to the temporal duration of migration, the length of migration, staging habitat enroute, competition for food on wintering and staging grounds and average environmental conditions on the breeding grounds during the prelaying and laying periods.

In contrast to the migration route, the wintering grounds of Dusky Geese offered abundant food resources and a mild climate. Dusky Geese evolved to take advantage of this situation by storing reserves on the wintering grounds to meet a large proportion of the energy needed during the reproductive season.

Energy Requirements

Calculations indicated food during migration may have provided about half of daily energy requirements, despite the major contribution from lipids. Although staging areas did not play the role apparently characteristic for arctic geese, they nevertheless were important to the energetics of Dusky Geese. At present, little knowledge exists on the location, use and security of staging areas frequented by spring migrating Dusky Canada Geese.

Prelaying and Egg Laying Periods

Duration of Prelaying Period

The prelaying period during all years for Dusky Geese was 13 to 18 days, equal to or longer than the period of rapid maturation of ovarian follicles (Grau 1976). Raveling (1978) suggested that Canada Geese initiated rapid maturation of follicles upon departure from the last major staging grounds enroute to the breeding grounds or upon arrival on the breeding grounds. In contrast, Ross' and Snow Geese initiate maturation of follicles considerably before leaving the last major staging grounds (Ryder 1967, Ankney and McInnes 1978). Dusky Geese appeared to initiate rapid follicular maturation immediately after arrival on the Copper River Delta possibly since early spring made food and nest sites available. Had spring conditions been later, Dusky Geese would probably have had the capability of delaying rapid maturation of follicles until conditions were favourable.

For geese such as Dusky Geese, which depend to a large degree upon food protein for replenishing reserves and for egg formation during the prelaying period, the ability to postpone rapid maturation of follicles until a ready protein source becomes available may be highly adaptive. This delay may only be possible for geese which nest at lower latitudes or in northern regions with maritime climates, where the growing season is longer than in the Arctic. On the other hand, Arctic nesting geese can not afford delays in nest initiation due to the brevity of the growing season with the possibility of an early and abrupt onslaught of severe weather (Barry 1982). Further, the timing of spring snowmelt on the Copper River Delta is highly variable, and may have required a mechanism in Dusky Geese that could account for such variation in availability of food and perhaps nest sites. The need for a protein source during the prelaying period and the relatively long growing season on the Copper River Delta may have promoted the ability in Dusky Geese to delay to some extent the period of rapid maturation of ovarian follicles until optimal conditions for egg formation occur.

Composition - Prelaying

Geese arrived on the delta with little change in protein reserves, but with a 52.2% reduction in lipid reserves (Table 6). Arctic geese are generally thought to experience a loss of reserves during the prelaying period (Barry 1962, 1966, Hanson 1962, Raveling and Lumsden 1977, Raveling 1978, 1979a, and others). However, few quantitative studies have been made to document such loss, nor have changes in carcass components during prelaying been examined. Barry (1966) recorded weight loss in Brant and Lesser Snow Geese after arrival on nesting grounds. Raveling (1979a, 1979b) unfortunately did not differentiate between arriving and prelaying Cackling Geese. The prelaying period is often only one to three days in Lesser Snow Geese, and Ankney and MacInnes (1978) did not measure changes in composition between arrival and initiation of laying.

Dusky Geese were probably able to increase their energy reserves before egg laying because early snowmelt each year of the study resulted in availability of nutritious forage on the nesting grounds. The increase in lipid reserves may be possible only during early springs as were characteristic of this study. Food appeared to be readily available when geese arrived on the breeding grounds each year. The use of nesting grounds for accumulation of protein, however, may be typical. This accumulation occurred as protein was deposited in developing follicles. Due to low food availability in late springs, geese would probably be less successful at procuring the amount of protein from food that I observed, while still laying the same number of eggs.

Composition - Egg Laying

Body weight of Dusky Geese peaked at initiation of egg laying, then declined 11.2% (406 g), of which 32.3% (131 g) was lipids (Table 6). Ankney and MacInnes (1978) observed a 14.2% (420 g) loss in body weight of Lesser Snow Geese between arrival and initiation of incubation; 28.8% (121 g) was accounted for by depletion of fat reserves. From "prelaying" (arrival) to initiation of incubation, Cackling Canada Geese lost 503 g or 26.7% body weight (Raveling 1979a). This constituted a substantial loss compared to the 11.2% and 14.2% loss observed in Dusky Geese and Lesser Snow Geese, and indicates a probable weight loss in Cackling Geese prior to egg laying as well as during laying.

I calculated the percent composition at initiation of incubation of Cackling Geese reported by Raveling (1979a) for comparison to percent composition of Dusky Geese at the same stage. Lipid content of Dusky and Cackling Canada Geese averaged 15.6% and 12.3% respectively, protein content was 18.9% and 19.6%, and water comprised 62.1% and 56.3%. Thus, based on small sample sizes, composition of Dusky and Cackling Canada Geese may have been similar at initiation of incubation during early springs of both studies. Comparisons during arrival and prelaying stages were not possible.

Lipid reserves of Dusky Geese increased between mid-laying and late laying stages (Table 6). King (1973) and Ricklefs (1974) discussed the decline in energy costs of egg formation soon after laying is initiated. Although small sample sizes precluded definitive conclusions, perhaps accumulation of lipids occurred because better feeding opportunities provided for increased energy intake while energy requirements of egg formation and other activity declined. A slight increase occurred in body weights reported for Lesser Snow Geese, Pacific Brant and White-fronted Geese at the end of laying (Barry 1966); this gain may have represented a similar lipid gain.

A rapid decline in lipid reserves occurred in Dusky Geese between late laying and initiation of incubation. Dusky Geese were also attentive to nests during late egg laying; they spent 95% of their time on the nest by the first day of incubation (unpubl. data). Cooper (1978) also found that Giant Canada Geese spent considerable time on the nest by late egg laying. Possibly the restriction in time available for feeding contributed to the loss of lipid reserves in Duskys observed between late laying and initiation of incubation.

Dusky Geese experienced a net loss of 66 g of protein, which represented 48% of their endogenous protein above the base level of 472 g, during egg laying (Table 8). Comparative data on absolute protein changes are not available for other geese. Ankney and MacInnes (1978) calculated a protein loss of 34 g using a protein reserve index for Lesser Snow Geese, an amount equivalent to 8.1% of the total weight lost during laying, but this did not include protein in the ovary as follicles developed and eggs were laid. In comparison, measured loss of protein in Dusky Geese accounted for 13.8% of the total weight lost during laying.

Carcass analysis indicated a slight increase of 20 g in protein reserves between late laying and initiation of incubation, but this may have been a result of a small sample of geese during the latter stage (n=4) rather than a real change. Unlike declining lipid needs (King 1972, Ricklefs 1974) protein requirements remain fairly constant throughout egg laying primarily because more than half of the protein content of waterfowl eggs is deposited in the albumen (calculated from Romanoff and Romanoff [1949]) during each egg laying interval. Rounding of percentages of other components used in calculating absolute amounts could have led to an error of this magnitude (less than 1% of body weight). Because the 20 g gain could not be explained and was based on a small sample, I concluded a real change was not indicated.

Carcass Composition and Clutch Size

There was an obvious drain on protein and lipid of Dusky Geese as laying progressed (Table 10). A similar drain of lipids was reported for Mallards (Krapu 1981) and both Lesser Snow Geese and Cackling Canada Geese lost substantial amounts of lipid and protein between arrival/prelaying and initiation of incubation (Ankney and MacInnes 1978, Raveling 1979a).

The lack of correlation between potential clutch size of Dusky Geese and absolute amounts of carcass components was unexpected. Ankney and MacInnes (1978) demonstrated a positive relationship between nutrient reserves and developing follicles in Lesser Snow Geese. They noted further that body weight of all Snow Geese was similar at initiation of incubation, regardless of clutch size. Weight of Dusky Geese at this stage were not the same. Possibly individual variation in size is greater in Dusky Geese than in Lesser Snow Geese, thus obscuring relationships between energy reserves and potential clutch size of individual geese. A relationship might exist during late springs when Dusky Geese would presumably have limited reserves compared to during more favourable early springs, such as those typical during this study.

Individual geese may also have varied in their capability or opportunity to supplement endogenous lipid and protein from environmental sources. Several authors suggested individual variation in the ability to store or supplement reserves may contribute to variations in clutch size. Jones and Ward (1976) observed that Red-billed Quelas (Quela quela) producing different size clutches varied in the rate at which reserves fell during egg formation. The opportunity to feed efficiently may also vary according to factors such as the aggressiveness of the gander in providing optimal time and opportunity for the goose to feed (Fox and Madsen 1981, Raveling 1982). Since Dusky Geese rely to a large extent upon food for the requirements of egg formation, particularly during years when food supplies are abundant, relationships between reserves and potential clutch size would be further obscured if the rate at which stored reserves were supplemented varied between individuals. Alternately, the same relationship should be more readily apparent in Lesser Snow Geese, as has been observed (Ankney and MacInnes 1978), because Lesser Snow Geese apparently rely more on reserves during egg laying than do Dusky Geese (Ankney 1977).

Food Availability

High availability of food on the nesting grounds of Dusky Geese during prelaying and laying periods was evident from the prelaying weight gain of geese, and from the large proportion of daily energy requirements provided by metabolism of food. Several authors suggested that food was not available or used by arctic nesting geese during the prelaying and laying periods. Ankney (1977) concluded that breeding Lesser Snow Geese fed little during egg laying. However, the digestive tracts of 68% of female Lesser Snow Geese collected during the arrival period were one-half to completely filled with food; 40% of female geese collected during egg laying contained similar amounts of food. These geese probably fed shortly before being collected as transit time of food in the digestive tract of geese was estimated at 1.5 hours (Harvey 1971 and Ankney 1977). Ely (1979) observed female White-fronted Geese fed 58% of the time during the prelaying period in western Alaska. On the north slope of Alaska female White-fronted Geese fed 68% of the time during the prelaying period (S.G. Simpson, USFWS), Anchorage, Alaska, pers. comm.). Also, Barry (1966) observed that female Lesser Snow Geese often wandered from their territories to feed during egg laying; these geese ate cranberries (_Vaccinium_ sp.) of the previous year and new growth of sedges. Pacific Brant recently arrived on nesting grounds were recorded feeding on debris and fronds of

Potamogeton vaginatus (Barry 1966). Raveling and Lumsden (1977) believed Interior Canada Geese did not feed during the period of egg formation. However, their conclusion was based on 5 geese with empty digestive tracts, collected on the breeding grounds during the arrival period but before the main arrival of geese and during a spring of delayed snowmelt. Their observation that geese used open water on a river and meltwater ponds, in the absence of snowfree ground, suggested access to some aquatic food existed, at least in the form of basal portions of grasses and sedges, and possibly aquatic plants. Hanson (1962) also suggested that Interior Canada Geese existed on stored reserves during prelaying and laying periods. However, 18 female geese weighed by Hanson at arrival averaged 4,188 g (± 109) whereas the 1 goose collected at egg laying weighed 4,930 g, indicating the possibility of a weight gain during the prelaying period in years of favourable conditions. Raveling (1979b) observed that there appeared to be little if any food available on the breeding grounds of Cackling Canada Geese, but calculated that 60% of the energy requirements of females (exclusive of the energy content of eggs) between "arrival" and initiation of incubation was derived from food. Barry (1962) observed that even during late springs some food was available and was utilized by Atlantic Brant. Fox and Madsen (1981) found that feeding constituted 68% of the diurnal activity of female

White-fronted Geese in Greenland during the prelaying period. Prior to clutch completion, Pink-footed Geese fed 8-9% of the time (Inglis 1977).

Possibly food quality (i.e. food with high protein content) is more important than food availability during prelaying and egg laying periods. Krapu (1979) reviewed studies of 5 species of ducks where the consumption of invertebrates by females increased during egg laying, purportedly in response to high protein needs. Duskys more than doubled endogenous protein during prelaying as follicles matured and derived almost 66% of their protein requirements during laying from food. Thus, high protein food played a critical role in fulfilling nutritional needs. Chapin *et al*. (1975) and Chapin *et al*. (1980) determined that nitrogen levels in arctic vegetation near Barrow, Alaska peaked within 10 days of snowmelt, and declined thereafter in both concentration and total amount. They noted that leaves of deciduous shrubs and inflorescences of *Salix* spp. and *Eriophorum* spp. were sources of highest concentrations of nitrogen, a measure of protein content. Chapin further suggested that herbivores that are protein limited should therefore select grasses or monocots early in the season. Harwood (1977) observed female Lesser Snow Geese feeding on monocotyledon roots after arrival on the breeding grounds. Esophagi of Dusky Geese examined from geese collected during laying and prelaying often contained

Equisetum sp. shoots and basal portions of *Carex* shoots (Bromley unpubl. data). Analysis of a sample of *Equisetum* shoots collected where geese have been foraging in early spring revealed a crude protein content of 21.2% of dry weight. Thus, Dusky geese consumed food of high protein content during these periods.

Further evidence of feeding on high quality foods, and the opportunity to do so is available from several studies in northern regions. Plant growth in arctic and alpine environments may take place even under snow with the photosynthetic capacities of plants, and their quality as food, increasing dramatically once ambient temperatures reach 0°C (Bliss 1962, Tieszen 1974). Thus, even in arctic environs, food quality rises rapidly as stored nutrients are mobilized from the roots to the apical parts of the plants. Although not discussed in the text, Figures 2 and 3 in Harwood (1977) showed that crude protein in monocots on nesting grounds of Lesser Snow Geese had peaked and were descending by late June. Snow Goose laying occurred in early June in that area, and probably coincided with the early peak in crude protein levels of plants. Similarly, Inglis (1977) noted that Pink-footed Geese fed on buds and leaves of dwarf willow (*Salix* spp.) during prelaying and egg laying, and that feeding activity of females peaked during establishment of nests when protein and energy needs were high. Dennis et al. (1978) tested selected plant species from the North Slope of Alaska and found Salix arctica leaves had the highest caloric content of those examined. In summary, new evidence has accrued indicating that egg laying geese utilize high protein and high energy plants, and time egg laying to coincide with the onset of rapid early growth of plants.

Although conflicting information exists on the availability and use of food by geese on northern nesting grounds during the prelaying and laying periods, the brief review of literature above suggested some food is almost always available and is used by geese. This food is probably high protein food. Additional quantitative studies are required during years of varying phenological conditions to elucidate the availability and use of food resources in different environments and by different species.

Although not studied during a late spring, food generally may be more available to Dusky Geese than to arctic nesting geese, because of the maritime climate of the Copper River Delta. Alternatively, geese may delay the period of rapid maturation of follicles until food becomes available. Because Duskys did not arrive with protein reserves beyond those retained for the costs of incubation, they must on average have a sufficiently high protein food source during the prelaying or egg laying period, or be able to draw further upon endogenous resources during springs of low availability of food to meet the requirements of egg formation. Additionally, food resources must provide an energy source that supplements lipid stores needed for egg formation and metabolic needs. By taking advantage of favourable conditions on their breeding grounds, Dusky Geese compensated for the high cost to lipid reserves of spring migration and the low protein reserves typical upon arrival.

Clutch Size

Lack (1967) believed clutch and egg size evolved in relation to the average availability of food to laying females. Ryder (1970), assumed arctic geese were independent of food during egg laying and proposed that clutch size ultimately depended on the amount of reserves a female could carry during spring migration. He suggested these reserves were allocated to an optimum number and size of eggs for maximum survival of young until they were able to feed, with sufficient reserves retained by the female to allow maximum attentiveness to eggs during incubation. MacInnes *et al*. (1974) believed stored reserves of geese varied annually and thus comprised a proximate factor limiting clutch size as well as an ultimate factor. Ankney and MacInnes (1978) similarly concluded clutch size of Lesser Snow Geese was determined by the size of nutrient (lipid, protein and calcium) reserves.

Dusky Geese arrived on the nesting grounds with protein reserves equivalent to the amount used during incubation.

Apparently, egg protein is normally derived solely from the nesting grounds, as geese would presumably not be able to predict conditions on the nesting grounds prior to departure from the Willamette Valley. Another possibility is that Duskys have the capability of withstanding further loss of protein during years with late springs than was observed during the early springs of this study. Lipid reserves upon arrival were only about 46 g (414 kcal) in excess of those retained for incubation. Thus, a large proportion of the energy requirements during prelaying and laying was derived from food. During this study, average clutch size (5.6 eggs) nearly equalled the maximum of 5.8 eggs (n=140) recorded for the subspecies in 13 years of study (Bromley 1976, Shepherd 1966, Timm 1973, Trainer 1959). From this I concluded geese were at or near their maximum potential for egg laying under natural conditions.

Protein requirements during laying were comprised of an average of 119.3 g used in formation of the clutch plus that used for maintenance metabolism. Robbins (1981) estimated endogenous loss of protein in birds as 0.60 $g/kg^{.75}/day$ and maintenance costs at 2.68 g/kg. Thus, protein need, exclusive of protein used in formation of the clutch was about 8.2 g/day, or 66 g for the 8-day egg laying period. Including clutch formation, 185 g protein were required during egg laying, of which 119 g or 64% was derived from food. Coincidentally, this was equal to the protein content of 5.6 eggs.

I suggest that annual variation in clutch size of geese is proximately limited by protein availability, both from body reserves and from food resources. In geese which characteristically experience a prelaying period of many days, food is potentially more important than in geese which have little time on nesting grounds before initiating egg laying. Although Dusky Geese apparently rely on food sources for the protein and lipids needed in the formation of the initial eggs of a clutch, arctic geese probably rely on endogenous protein for the initial eggs. During early seasons of high availability of food, Duskys increase endogenous protein during prelaying, probably for deposition in developing follicles. Similarly, in favourable seasons, arctic geese probably minimize loss of protein or even increase endogenous protein. These supplements, in both Dusky and arctic geese, may account for an increase of up to 1 or 2 eggs in the average clutch during favourable years. Clutch sizes of Dusky Geese have varied by up to 2.5 eggs annually (between 3.3 and 5.8) (Timm 1973, Shepherd 1966). Average clutch sizes in arctic geese vary by up to 2 eggs annually (Barry 1966, MacInnes *et al*. 1974, Raveling and Lumsden 1977, Dau and Mickelson 1979, and others). Barry (1966) noted Lesser Snow Geese, Pacific Brant and White-fronted Geese spent less time feeding during late springs than early or average springs. In late springs, clutches would be reduced to the minimum number of eggs that could be produced from protein reserves present upon arrival of arctic geese. In Dusky Geese, protein intake is restricted and the clutch is reduced in late springs. Either some protein from food must always be available to Dusky Geese, even in late springs, because protein reserves present upon arrival were insufficient for production of even a few eggs, or the minimal level of protein content observed did not represent the minimum level that could occur during years of unfavourable conditions. In a study of White-fronted Geese in western Alaska, Ely (1979) similarly concluded that feeding is of utmost importance if females are to lay maximum clutches. Jones and Ward (1976) concluded that clutch size of Red-billed Quelas was regulated by stored reserves, particularly protein reserves, and by the rate at which those reserves could be supplemented from food sources.

Raveling (1979b), contended that no food was available to Cackling Geese, but recognized that amount and quality of food available during prelaying and laying were variable and could affect clutch size. Ryder (1970) observed that during the egg laying period Ross' Geese occasionally visited mainland marshes typically used for feeding, but did not believe they were feeding at that time. As was suggested for Red-billed Quelas (Jones and Ward 1976, 1979) and Mallards (Krapu 1981), arctic geese may experience an energetic loss while procuring high protein food. Since low availability of food may be typical of arctic nesting grounds, geese may deplete lipid reserves while searching out high protein food, particularly during the laying period. The energetically inefficient use of lipids for gathering protein has been discussed for Mallards (Krapu 1981) and Grey-backed Camaroptera (Camaroptera brevicaudata) (Fogden and Fogden 1981). During years of relatively high availability of food, endogenous protein could be supplemented by geese at less cost to lipid reserves, freeing lipids for deposition in extra eggs.

Duskys terminated egg laying at a point where considerable energy reserves were retained to meet the requirements of incubation, as has been observed for other geese (Ryder 1970, MacInnes *et al*. 1974, Ankney and MacInnes 1978, Raveling 1979a). Several authors noted that body weights of both geese and eiders (which have a similar energetic strategy of reproduction) at initiation were similar to body weights during mid-winter (Ankney 1974, Korschgen 1977, Raveling 1979a). Body weight of Duskys at initiation of incubation (3,206 g) was similar to weights during mid-winter in the mid-1960's ($\bar{x}$ = 3,251, n=21, Chapman 1970) but more than in the mid-1970's ($\bar{x}$ = 2,912, n=30, Bromley unpubl. ms.). Raveling and Lumsden (1977) termed the mid-winter weight a "basal" winter weight, and believed the correlation with weight at initiation of incubation constituted a mechanism for the cessation of laying in geese. Raveling (1979a) further suggested that when protein reserves were depleted to that level retained for incubation, laying ceased. My data agree with this suggestion but indicate that dietary protein as well as protein reserves influence clutch size.

Incubation

Body Weight

Dusky Geese retained lipid and protein reserves during egg laying which were used during incubation, as noted in other geese (Barry 1966, Ryder 1970, Ankney and MacInnes 1978, Raveling 1979a) and Common Eiders (Korschgen 1977). Duskys lost 22.2% (711 g) of their body weight during incubation (Table 6), similar to the 21.2% loss recorded in Cackling Geese (Raveling 1979a) but less than the 32% lost by Lesser Snow Geese (Ankney and MacInnes 1978) and Common Eiders (Korschgen 1977) during incubation.

Lipids

Loss of lipids in Duskys accounted for 54.4% (387 g) of weight loss (Table 6) compared to 47.3% in Cackling Geese (Raveling 1979a) and 55.6% in Common Eiders (Korschgen 1977). Depletion of large lipid stores by the end of incubation was also recorded in Lesser Snow Geese (Ankney and MacInnes 1978). Ryder proposed that large energy reserves retained during egg laying allowed geese to give maximum attentiveness to eggs during incubation. Duskys displayed a similar pattern of retaining energy reserves during egg laying and expending those reserves during incubation. Thus, while Duskys altered their energetic strategy to compensate for lowered lipid and protein reserves upon arrival on nesting grounds by relying on food resources, the need for stored energy reserves during incubation remained.

Protein

Loss of protein accounted for 10.1% of the loss of body weight during incubation (Table 6). Raveling (1979a) estimated that loss of protein accounted for 7.9% of weight loss in Cackling Geese. A considerable decline of protein reserves was also indicated for Lesser Snow Geese during incubation (Ankney and MacInnes 1978).

Benedict and Lee (1937) and Hanson (1962) discussed the need of a fasting goose to metabolize body protein concurrently with fat. Raveling (1979a) noted that fat reserves in 2 geese collected at mid-incubation were considerably reduced, while loss of protein reserves had not yet occurred. He concluded that during the fast of incubation, metabolism of body protein may not be needed to supply the oxaloacetate necessary for metabolism of stored lipids, at least to the degree suggested by Hanson (1962).

The difference in conclusions regarding use and need of protein reserves by geese may stem from the erroneous assumption that incubating geese were fasting.

Common Eiders, at midpoint of incubation (Korschgen 1977) weighed 31% less than Dusky Geese and 42% more than Cackling Geese, yet they lost 40.8% and 80.8% more protein than Dusky and Cackling Canada Geese, respectively. I believe the disproportionate loss occurred because Eiders did not feed during incubation (Korschgen 1977) but Canada Geese did. Applying Robbins' (1981) formulae for estimating maintenance needs for protein, I calculated a 2.17 kg Eider required 152 g of protein during the 26 day incubation period. Although a slight overestimate of the measured 120 g loss, the theoretical calculation was similar. The overestimate may be attributable to Allison's (1959) observation that relatively less protein was required to achieve nitrogen equilibrium in the depleted animal. Applying Robbins' formulae to Dusky Geese, an estimated 194 g of protein would be required. Of this, body reserves supplied 71 g, leaving a need for 123 g or 4.6 g/day. Ebbinge _et al_. (1975) estimated Barnacle Geese (_Branta leucopsis_) consumed 158 g (dry weight) of forage in 7 h, or 22.6 g/h. Since Dusky Geese are more than 40% larger I assumed Dusky Geese could procure 30 g/h of forage. Food items collected on the nesting grounds that were frequently found in esophagi of geese collected during incubation contained about 25% crude protein (dry weight). With these assumptions and conditions, and an assimilation efficiency of 0.6 for young terrestrial vegetation (Ricklefs 1974), Dusky Geese could meet their protein requirements by foraging an average of 58 min/day. If protein needs were overestimated, as occurred with Common Eiders, less feeding time would be necessary. Based on 217 days of time lapse photography, I estimated Dusky Geese were off their nests at least 1.8 h/day (Part II of this study). Thus, sufficient time for procurring 4.6 g of protein per day by feeding was available to incubating geese. Common Eiders, in contrast to Dusky and Cackling Geese, were apparently completely independent of food during the laying and incubation periods (Korschgen 1977). As a result, they must have relied almost completely upon catabolism of lipids and gluconeogenesis to meet energy needs, thereby depleting lipid and protein reserves to a much larger extent than did Canada Geese. The decline of 24% in the protein reserve index for Lesser snow Geese (Ankney and MacInnes 1978) although absolute values cannot be directly inferred, indicated that Snow Geese similarly experienced a greater degradation of protein than did Canada Geese. However, an alternative hypothesis is that Canada Geese might also have the capability of drawing upon body protein to a greater extent than has been observed in studies to date.

Energy Requirements

I calculated that 66.1% of daily energy requirements of Dusky Geese during incubation were met by energy reserves, and 33.9% of requirements were derived from food (Table 11). Comparative figures for Cackling Geese were 48% from reserves and 52% from food (Raveling 1979a). The contribution and need of essential amino acids from food is unknown, but may be critical (Allison 1959). A detailed discussion of the chronology and use of stored reserves and food during incubation is the subject of another report (Part II of this study).

General

In the foregoing discussion it was demonstrated that there can be gross differences in the energetic strategies of migration and reproduction in different species of geese, and even subspecies of Canada Geese. An example of this was the large drain on lipid reserves of Dusky Canada Geese during migration not experienced by most other taxa studied to date. Researchers are cautioned not to extrapolate composition data from one taxa to another at least until the energetic strategies of the two have been studied in detail and found to be the same.

Similarly, although body weight often correlated well with energy reserves, it cannot be relied upon as an indicator of condition in geese. For example, mean body weight of dusky Geese peaked at 3,627 g at initiation of egg laying when energy reserves were 43.7% below peak reserves at a body weight of 3,512 g (Table 6). Also, a weight loss of 11% during migration corresponded to a decline of 51% of energy reserves. These phenomena occurred because of a tendancy for lipid reserves to be replaced by water as they were metabolized or to replace water as they were stored during migration and the early stages of reproduction. Milne (1976) noted that water yielded from catabolism of fat may help to restore water balance in fasting Eiders. A similar situation may have occurred with Dusky Geese during the migration and incubation periods.

Since geese were studied only during early springs, it is possible that some of the residual lipids remaining at the end of the incubation period could have been drawn upon further. Although the amount would be small, study of lipid reserves during a phenologically late spring would clarify this possibility.

As stated previously, I assumed that protein levels in adult female Duskys at hatching of eggs were minimum levels of protein required for the basic structure of the living goose. It would be surprising, however, to observe members of such closely related taxa as Canada Geese, Snow Geese and Common Eiders having such widely varying capabilities to withstand loss of protein. After comparing protein losses of Duskys to that of Common Eiders and Lesser Snow Geese, I conclude protein levels of Duskys at hatching may not have reached the minumum levels possible in living geese. Studies of protein levels during starvation or years of low food availability (late springs) are necessary to determine the actual level of protein necessary in functioning adult female Dusky Geese.

Part II: INCUBATION BY CANADA GEESE: THE RELATIONSHIP OF ENERGETICS AND BEHAVIOUR TO LIFE HISTORY TRAITS

INTRODUCTION

Recognition of the interdependency of various stages of life history is an important step towards understanding the evolution of different patterns of reproductive strategies of birds. Birds have evolved specific adaptations to minimize heat loss from eggs while maximizing heat transfer to them. Such adaptations indicate the importance of incubation strategies in influencing or being influenced by other stages of the reproductive cycle (Ricklefs 1974). To contribute to the understanding of this relationship, I studied the energetic strategy and behavioural pattern of incubation of female Dusky Canada Geese (*Branta canadensis occidentalis*) and their use of endogenous and exogenous (environmental) energy sources to meet energy requirements.

Although earlier work on arctic nesting geese assumed geese were independent of food during incubation and that clutch size of female nidifugous birds was influenced by the need to retain sufficient reserves for incubation (e.g. Ryder 1970, Klomp 1970) subsequent studies have concluded that food energy may contribute over 30% of the energy requirements of incubation in geese (Raveling 1979b, Part I, this report).

How and when geese utilize environmental energy compared to endogenous reserves may be important. Drent (1973) noted the need to examine the influence of foraging routines on incubation behaviour of birds. In designing this study, I subscribed to the reasoning of Drent and Daan (1980:226) who advocated:

> "an approach emphasizing proximate controls exerted by local food supply on reproductive performance as an avenue towards understanding the shaping of the breeding pattern of the species by food supply as an ultimate factor defining survival value."

The goal of the research was to describe the patterns of energy use by female Dusky Canada Geese during the incubation period and the relationship of this pattern to: (a) other characteristics of the incubation period and (b) other stages of their life history. Objectives were to:

1) measure energy reserves of geese at initiation of incubation and at hatching,
2) determine changes in body weight throughout incubation,
3) determine characteristics of incubation behaviour,
4) document the timing of nesting, and
5) determine the food plants used and their proportions in the diet of incubating geese.

METHODS

Study Area

Dusky Canada Geese nest almost exclusively on the west side of the Copper River Delta in South-Central Alaska (Fig. 1). The geological and biological features of the Delta have been described in detail (Reimnitz 1972, Potyondy et al. 1975, Bromley 1976). Observations of geese were concentrated on the area having the highest density of goose nests on the Delta.

Behaviour of Incubating Geese

Incubation behaviour of female Dusky Canada Geese was recorded with time lapse photography in 1977, 1978 and 1979. Three Super 8 mm movie cameras exposed frames automatically each 1 to 2 minutes. Each camera was focused on one nest for a three day period, then moved to a second then third nest for similar periods, and finally back to the original nest to begin the cycle again. Thus, ideally, each of nine nests was photographed on a minimum of nine days distributed throughout the incubation period. However, due to abandonment and predation on clutches some nests were filmed on more than nine days while others were filmed on fewer days. Filmed nests included samples of nests initiated on different dates but excluded renests. Data were lumped by day of incubation over all years for statistical analysis. The incubation period was divided into three stages: (1) Day 0 (day last egg was laid) to Day 10; (2) Day 11 to Day 20; (3) Day 21 to Day 29. The incubation period (day last egg laid to day first egg hatched) averaged 27.5 days (Bromley in press), and ranged between 26 and 29 days.

Constancy of incubation was defined as the percent of time the female spent on the nest during an observation day. This day was always less than 24 hours, because behaviour of geese during the 3 to 5 hour period of darkness was not recorded, and because the time of day at which filming was initiated varied. Only those recesses (the entire period of absense as defined by Skutch 1962) that were recorded from beginning to end were considered in analysis.

Changes in constancy of incubation, average number of recesses per incubation day and average daily length of recesses over the incubation period were compared between females that hatched eggs and those that abandoned nests. Since most geese that abandoned nests had done so by Day 14 of the incubation period, only the first 13 days of incubation behaviour were analyzed for this group of geese. Behaviour during the first 13 days of incubation between geese which abandoned nests and geese that went on to successfully complete the incubation period. ?

Body Weight and Energy Reserves

Incubating geese were trapped throughout incubation using modified nest traps (Weller 1957). Geese were weighed to the nearest 10 g. Birds were trapped on nests of known history so that the day of incubation when trapped was known.

Data on energy reserves (stored lipid and protein that can be drawn upon without causing death) and carcass composition for geese collected at initiation of incubation and near hatching were reported earlier (Part I), and are drawn on again in this section. Additionally, data on lipid and protein reserves for one goose collected on Day 13 of the incubation period are reported here for the first time.

Availability, Quality and Use of Food

Frequency of food items from the esophagi was determined for incubating geese shot at hatching. The dry weight of each food item present in esophagi and that weighed over 0.25 g net weight was calculated by assuming 15% water content for seeds and 80% water content for all other food items (averaged from Cummins and Wuycheck 1971). Raveling (1979b) estimated Cackling Canada Geese (*B. c. minima*) fed on seeds at the rate of 43 g dry weight/h. Since Dusky Geese are about 100% larger than Cackling Geese, I estimated Duskys would obtain seeds at the rate of at least 50 g/h.

Ebbinge et al. (1975) estimated Barnacle Geese (*B. leucopsis*) obtained green forage on wintering grounds at the rate of 22 g/h dry weight, and Raveling estimated a rate of 25 g/h for Cackling Geese (Raveling 1979b). Again, since Dusky Geese are larger than those geese, I used a feeding rate of 30 g/h for Dusky Geese.

The dry weights of all food items in the esophagi were lumped, and the proportion of each food item was used to represent the proportion of each food item in the diet. Assuming that in one hour of feeding, the amount of each food item obtained corresponded to the proportion found in the diet, and the feeding rate for that food item, I calculated the grams of each food item that would be obtained on average in one hour of foraging. The weight of each food item that would be obtained was then multiplied by its caloric content (Cummins and Wuycheck 1971) and by the assimilation efficiency of 0.33 (Owens 1972, Ebbinge et al. 1975) for green forage and of 0.80 for seeds (Ricklefs 1974) to obtain the metabolizable energy obtained per hour of foraging.

Availability of food was assessed subjectively, based on daily observations of development of green forage plants through the incubation period, and records from time lapse photography.

Miscellaneous

Weather data originated from the Cordova Airport FAA station 12 km north of the study area (USDC 1977-1979). Statistical procedures followed Nie et al. (1975), Tuccy (1980) and Holen (1979).

RESULTS

Timing of Nesting

Geese arrived on the nesting grounds at similar times each year (Table 2). Peak arrivals were observed on 19, 17 and 21 April for 1977 through 1979, respectively.

Initiation dates of 460 nests were determined. Initiation of nests peaked each year between 4 and 6 May (Fig. 5). The temporal pattern of nest initiation was not the same in all years (Median $X^2=61.9$, $P<0.001$), but geese were highly synchronized in initiation of nests. All 3 years were considered phenologically early (cf. Bromley 1976 and Part I of this study).

Incubation Behaviour of Geese

Behaviour of 14 successful geese was recorded on 122 days for periods from 6.0 to 20.8 h ($\bar{x}=16.2$ h) per observation day. No difference in constancy of incubation by geese was detected between the first two stages of the incubation period; however, geese spent more time off the nest during the last nine days of incubation ($P<0.05$, Table 13). Concomitantly, the number of recesses per observation day and the average length of recesses remained the same during the first two thirds of incubation but were greater during the last third ($P<0.05$, Table 13). Geese were off nests an average of 1.7 h/day during the first 20 days and

Figure 5. Pattern of dates of nest initiation by Dusky Canada Geese on the Copper River Delta, Alaska from 1977 to 1979.

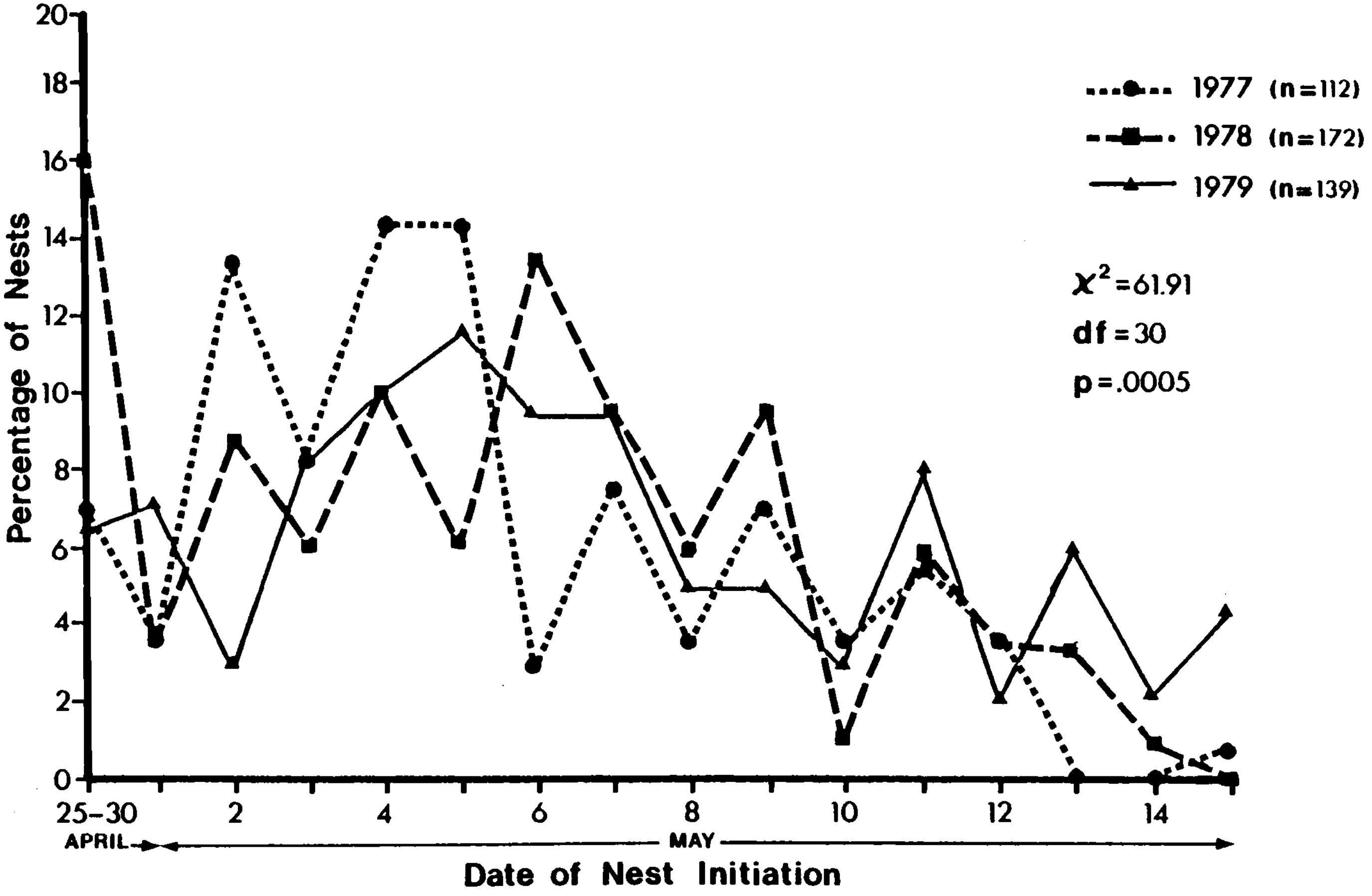


Table 13. Changes in constancy of incubation, average number of recesses per day, and average recess length for Dusky Canada Geese between early, mid and late incubation.

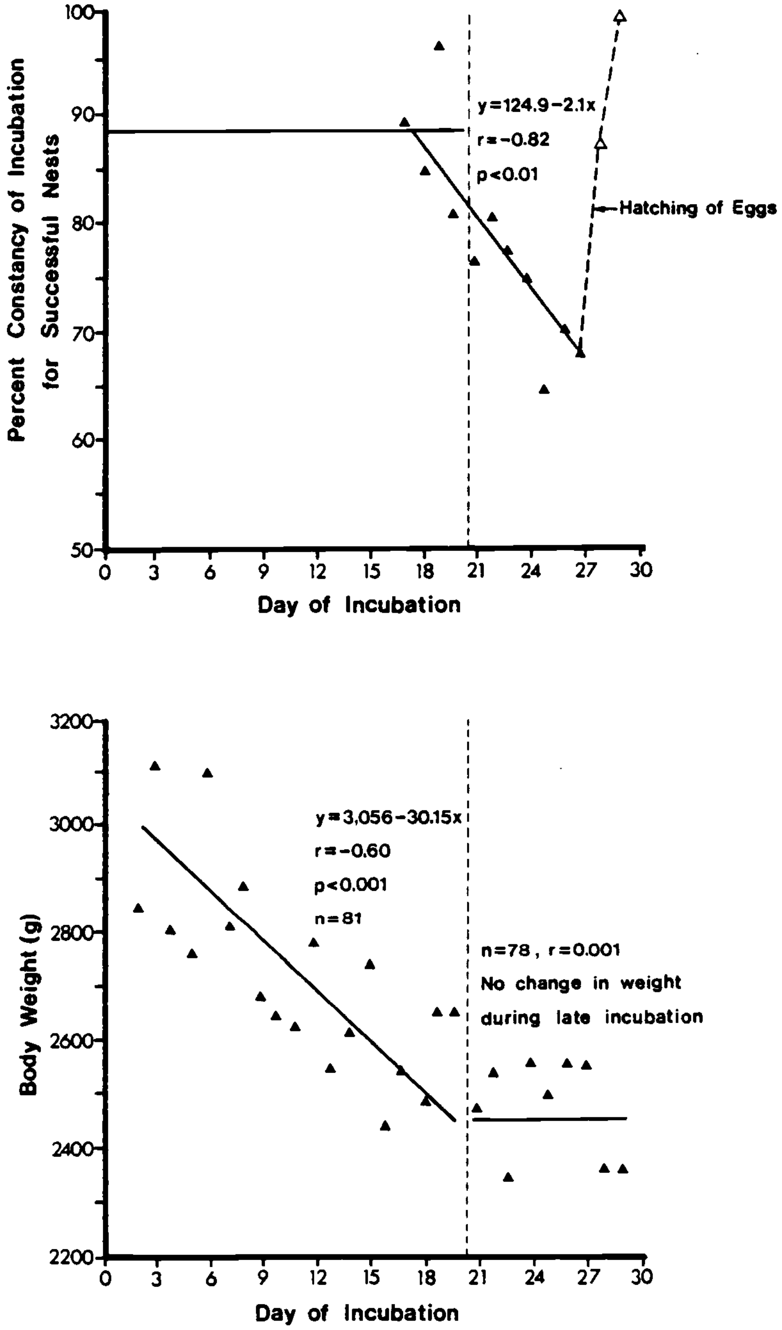
	Stage 1 Days 0 to 10			Stage 2 Days 11 to 20			Stage 3 Days 21 to 29			SNK ($p \leq 0.05$)[a] Incubation stage
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	
Constancy of[b] incubation	89.5	0.09	31	88.2	0.04	45	78.6	0.09	43	1+2 the same 3 different
Mean daily[b] length of recesses (min)	19.5	1.8	31	19.7	1.5	45	26.5	1.8	43	1+2 the same 3 different
Mean daily[b] number of recesses	4.3	0.54	31	5.0	0.45	45	6.5	0.54	43	1+2 the same 3 different

[a] SNK is the Student-Newman Keuls a priori contrast test for differences between groups.

[b] The results of a 1-way analysis of variance were: $F=9.6$, d.f.=2,116, and $p<0.001$ for constancy of incubation; $F=5.7$, d.f.=2,116, and $p<0.005$ for mean daily length of recesses; and $F=4.6$, d.f.=2,116, and $p<0.05$ for mean daily number of recesses..

Figure 6. Relationship of (a) constancy of incubation and (b) body weight to the day of incubation for female Dusky Canada Geese.

Figure 6.


100
90
80
70
60
50
Percent Constancy of Incubation for Successful Nests
y=124.9-2.1x
r=-0.82
p<0.01
Hatching of Eggs
0
3
6
9
12
15
18
21
24
27
30
Day of Incubation
3200
3000
2800
2600
2400
2200
Body Weight (g)
y=3,056-30.15x
r=-0.60
p<0.001
n=81
n=78, r=0.001
No change in weight
during late incubation
0
3
6
9
12
15
18
21
24
27
30
Day of Incubation

3.5 h/day during late incubation (Fig. 6a). Thus, successful geese spent twice as much time off the nest during late incubation as during early and mid-incubation. However, geese were attentive at the nest during hatching of eggs, as was expected (Fig. 6a).

Five geese which abandoned their nests were observed on 18 days during the first 13 days of incubation, for an average of 15.5 h (SE=1.1 h) per observation day. Incubation constancy of unsuccessful geese declined throughout the first 13 days of incubation ($r=0.40$, $P<0.10$, Table 14) while geese whose eggs eventually hatched had a constant level of attentiveness. Also, geese that abandoned their nests took increasing numbers of recesses during the first 13 days of incubation ($r=0.52$, $P<0.03$) while other geese did not (Table 14). Both groups of geese continued to take constant average lengths of recesses through the first 13 days of incubation.

Body Weight

One hundred and fifteen geese were trapped a total of 159 times between Day 1 and Day 29 of incubation over the three reproductive seasons. Comparison of annual linear regression lines of body weight by day of incubation revealed no difference between years ($P>0.25$, $F=1.59$, df=2, 154). Thus, data on body weight were pooled for the 3 years (Fig. 6b). Body weight declined rapidly early in

Table 14. Regression of characteristics of incubation behaviour by day of incubation during the first 13 days of incubation for successful geese and for those which eventually abandoned their nests.

	Successful geese		Unsuccessful geese		
Regression	Regression coefficient	Level of significance	Regression equation (n)	Regression coefficient	Level of significance
Constancy of incubation[a] by incubation day	0.06	NS	$y^b=1.352-0.124x$ (18)	0.40	0.05
Number of recesses by incubation day	0.01	NS	$y^c=1.82+0.229x$ (18)	0.52	0.01
Average length of recesses by incubation day	0.18	NS	-- (18)	0.02	NS

[a] Percent constancy of incubation was tranformed by the arc sine according to Nie et al. (1975).

[b] y = transformed constancy of incubation on incubation day x.

[c] y = number of recesses on incubation day x.

incubation, then gradually leveled out. The rate of weight loss was near zero by late incubation. A curvilinear relationship between weight (y) and day of incubation (x) was apparent ($y=3080-178.4 \ln x$, $r=0.51$, $P<0.001$).

During the first 20 days of incubation, body weight declined at a rate of about 16.6 g/day ($r=0.43$, $P<0.001$). No relationship between body weight and day of incubation existed during the last nine days of incubation (Fig. 6b). I concluded all or most loss of weight by incubating geese occurred by Day 20 of the incubation period, the same period during which nest attentiveness remained constant.

Dynamics of Stored Energy Reserves

Lipid content of geese declined an average of 307 g from initiation of incubation to hatching (Table 15). One goose collected on Day 13 of incubation had only 19% (73 g) of the average lipid content (387 g) present at initiation of incubation (Table 15). Thus, about 80% of stored energy reserves were utilized by about halfway through the incubation period.

In Part I of this study I estimated daily energy needs of incubating Dusky Geese at 198 kcal/day. The goose collected on Day 13 of incubation had a calculated reserve of 756 kcal (Table 15) indicating sufficient reserves remained for about 4 days of constant incubation.

Table 15. Body weights and components of adult female Dusky Canada Geese collected at initiation of incubation, mid-incubation and hatching on the Copper River Delta, Alaska from 1977 to 1979.

	Incubation			Mid-incubation		Hatching		
	$\bar{x}$	SD	n	Data point	n	$\bar{x}$	SD	n
Body weight(g)	3206	208	8	2690	1	2495	190	39
Lipid (g)	450	106	8	136	1	63	34	39
Protein (g)	543	46	8	495	1	472	48	39
Water (g)	1790	105	8	1749	1	1601	132	39
Lipid (%)	15.6	3.0	8	5.5	1	2.8	1.4	39
Protein (%)	18.9	1.6	8	19.9	1	20.8	1.5	39
Water (%)	62.1	2.1	8	68.7	1	70.6	1.9	39
Reserve kcal (%)[a]	3787	993	8	756	1	0	429	39

[a] calculated as the energy yield from catabolism of stored lipid (9.0 kcal/g) and protein (4.3 kcal/g) (Ricklefs 1974).

Food Habits

Food plants appeared to be readily available during all three years. Snow melt was complete before egg laying commenced and weather conditions were mild relative to long term averages (Tables 1 and 2). New shoots of sedges were available during prelaying and egg laying, and leaves of shrubs were readily available by mid to late incubation. In general, availability of forage appeared to increase from the time of arrival of geese on the nesting grounds to at least the end of incubation. By 1 June, new *Carex* spp. around nest sites were about as tall as geese sitting on nests, and were sufficiently dense to hide an incubating goose from observers 25 m away. Shrub leaves (*Salix* spp., *Alnus* sp., and *Myrica gale*) were completely unfurled by early June.

Twelve of 39 geese collected near hatching contained five different food items in amounts greater than 0.25 g dry weight (Table 16). *Carex* spp. seeds comprised over 50% dry weight of the diet, and contained about 75% of the metabolizable energy in the average diet of these 12 incubating geese.

Weather During Incubation

Weather conditions became gradually milder throughout the incubation period (Table 17). Minimum daily

Table 16. Food habits of 12 adult female Dusky Canada Geese and calculations of the number of kcal/h of feeding that could reasonably be assimilated for adult female geese during late incubation on the Copper River Delta, Alaska[a].

Food item	Frequency	$\bar{x}$(g)	SE	Total dry weight	Proportion of diet (dry weight)	g/h	Energy content kcal/g[b]	kcal/h
Carex spp. leaves	9	0.8	0.6	7.2	0.196	7.4	4.9	12.0
Carex spp. seeds	7	2.8	2.7	19.6	0.534	20.9	4.7	78.6
Equisetum sp.	7	0.7	1.1	4.9	0.134	5.0	4.0	6.6
Salix arctica	7	0.6	0.5	4.2	0.114	4.3	5.0	7.1
Lathyrus sp.	4	0.2	0.1	0.8	0.022	0.8	4.7	1.2
Total				36.7	1.000	38.4	105.5	

[a] At the feeding rate of 50 g/h, 0.4074 h are needed to provide 0.534 of the diet, consisting of seeds.
At the feeding rate of 30 g/h, 0.5924 h are needed to provide 0.466 of the diet, consisting of other plants.
For *Lathyrus* sp. the amount calculated is as follows:
0.022/0.466 (0.5924)(30)=0.8
To determine kcal/h from this food item, multiply by the caloric value and the assimilation efficiency as follows: 0.8(4.7)(0.33)=1.2 kcal/h.

[b] from Cummins and Wuycheck (1971).

Table 17. Summary of average weather parameters measured 13 km NW of the study area, at the Cordova, Alaska Federal Aviation Administration Station, 1977 to 1979 (from USDI 1977 to 1979).

	Weather Parameters 1977 - 1979 combined	
Parameter	10-20 May (early incubation)	6-16 June (late incubation)
Minimum temperature °C(SD)	2.0 (3.1)	6.0 (3.1)
Maximum temperature	11.4 (3.6)	14.9 (3.4)
Precipitation (in)	0.33 (0.51)	0.43 (0.94)
Wind speed (km)	4.5 (2.4)	3.0 (1.3)
Relative humidity (%)	75.5 (9.4)	79.5 (8.1)
Cloud cover (%)	71.8 (31.9)	77.6 (32.5)
Hours below freezing	1.0 (1.7)	0.3 (0.17)

temperatures and maximum daily temperatures rose an average of 7.2°F (4.5°C) and 6.4°F (4.0°C), respectively between early and late incubation. Average daily precipitation, relative humidity, and per cent cloud cover increased slightly between early and late incubation, while wind speed and hours per day below freezing declined.

DISCUSSION

Availability of food, especially to young, and to a lesser extent to the laying female, and the risk of predation on eggs, young and parents were identified by Lack (1968) as the primary selective pressures regulating characteristics of reproductive strategies in birds. Thus, laying date, clutch size and characteristics of incubation, as important parameters of reproduction in northern nesting geese, should be influenced by these forces. Based on observations of Dusky Canada Geese, I believe that environmental food resources at approximately two thirds through incubation are critical to nesting geese. I further suggest that the availability of these food resources played an ultimate role in the evolution of the timing of nesting, energetic strategy of incubation and clutch size in northern geese.

Body Weight and Energy Reserves

Incubating Dusky Geese experienced several conditions (discussed below) by one half to two thirds through incubation, which may be characteristic (though to varying degrees) of all northern nesting geese. One condition was a rapid decline in body weight to considerably reduced levels.

Weight loss during the incubation period has been quantified for Canada Geese (Raveling 1979b, Aldrich and

Raveling 1983, this study), Ross' Geese (*Chen rossii*) (Ryder 1967) Pacific Brant (*Branta bernicla nigricans*) and Whitefronted Geese (*Anser albifrons*) (Barry 1967),? Lesser Snow Geese (*A. caerulescens caerulescens*) (Barry 1967,? Harvey 1971, Ankney and MacInnes 1978) Barnacle Geese (Lessels et al. 1979), and other species of waterfowl (Harris 1970, Korschgen 1977, Krapu 1979, 1981 and others). Average loss of weight in geese ranged from 21.1% for Cackling Canada Geese (Raveling 1979a) to 32.4% for Lesser Snow Geese (Ankney and MacInnes 1978). Dusky Canada Geese lost 22.2% of their body weight during incubation.

Few investigators monitored patterns of weight loss during incubation. Krapu (1981) found a curvilinear relationship that described a rapid decline in body weights during the first week of incubation followed by a leveling off thereafter in Mallards (*Anas platyrhynchos*). The early decline was caused by rapid depletion of lipid reserves. Korschgen (1977) however, found that a linear model best described declining body weights of Common Eiders (*Somateria mollissima*) during incubation. Eiders, which lost 32% body weight during incubation, did not completly deplete lipid and protein stores until hatching (Milne 1976, Korschgen 1977). Protein reserves utilized were considerably greater for Eiders than for Canada Geese. This greater use of endogenous protein, combined with relatively larger lipid reserves, perhaps allowed Eiders to be nearly constantly attentive to eggs throughout the laying and incubation periods (Korschgen 1977).

Energy reserves in most incubating northern geese may be almost completely depleted by about two thirds through incubation. Mori (1977) observed significantly lowered blood serum protein and albumin in Interior Canada Geese (*B. c. interior*) collected during late incubation and concluded that lipid reserves had been depleted to the point where protein reserves were being tapped. Loss of almost all visible fat reserves in Interior Canada Geese by early incubation was reported by Hanson (1962). Depletion of lipid reserves in early incubation was recorded for Blue-winged Teal (*Anas discors*) (Harris 1970) and Mallard (Krapu 1981). The greatly lowered body weights of geese (Dusky and Cackling Canada Geese) and the energy reserves in a small number of collected geese (Dusky and Cackling) measured at mid-incubation indicated reserves of geese were severely reduced by mid to late incubation.

The one Dusky Goose collected in mid-incubation had estimated energy reserves sufficient for constant incubation through incubation Day 17. Two Cackling Geese collected at mid-incubation (about Day 13) by Raveling (1979b) had lost 66% of the average weight lost during the entire incubation period (my calculations). Energy reserves of these geese, calculated from information in Raveling (1979a) would have provided sufficient energy for four days of constant incubation at 108 kcal/day (Raveling 1979b). Thus, energy reserves of the two Cackling Geese would have been depleted at approximately Day 17 of the 26 Day incubation period, assuming constant incubation (my calculations).

Death from starvation was observed for considerable numbers of incubating Lesser Snow Geese (Harvey 1971, Ankney and MacInnes 1978) and for European Eiders (Milne in Korschgen 1977) indicating complete loss of reserves prior to or by the time eggs hatch. Because of the combined effects of egg predation, chilling of embryos causing death, and starvation of the female, natural selection should favour geese that leave the nest to feed a minimal, but sufficient, amount of time during late incubation to both incubate the eggs to hatching and to ensure their own survival for future reproductive efforts.

Constancy of Incubation

Incubation behaviour in birds, specifically high attentiveness to eggs, probably evolved in response to the need to protect eggs from environmental extremes, energy demands of the parents, and protection of eggs from predation (Drent 1967).? Environmental temperatures below freezing were a frequent occurrence during incubation periods of northern nesting geese (Table 17; Barry 1962, 1967; Ankney and MacInnes 1978). Ryder (1970), Ankney and MacInnes (1978) and Raveling (1979b) believed energetic cost of incubation in geese was derived almost entirely from stored reserves; however, Raveling (1979b) and I (Part I) estimated over 30% of the energy needs of incubating female Canada Geese was derived directly from food. Several observers reported increased predation on eggs associated with lowered nest attentiveness, and concluded high constancy of incubation in Geese and Eiders evolved particularly in response to egg predators (Milne 1976, Inglis 1977, Raveling and Lumsden 1977).

Dusky Geese were off nests more than twice as long during the last third of incubation compared to the first two thirds. Considerable evidence has accrued that a similar relationship characterizes other waterfowl. Although Cooper (1978) found no significant difference in amount of time spent off the nest per day by Giant Canada Geese (B. c. maxima) during late incubation compared to early incubation, average time off the nest was slightly longer during the last third of incubation. Giant Canada Geese spent an average of 19 min/day off the nest. Aldrich and Raveling (1983) observed 97.5% incubation constancy for captive Canada Geese, with less attentiveness as incubation progressed. Substantial increases in time off the nests were noted during the last week of incubation. Pink-footed Geese (Anser brachyrhynchus) spent more time off the nest during the last eight days of incubation compared to early and mid-incubation (Inglis 1977). Most egg loss from Lesser

Snow Goose nests occurred during late incubation (Harvey 1971) suggesting lower attentiveness to eggs than during early to mid-incubation. Barry (1967) reported Lesser Snow Geese left nests to feed at least once a day, and Brant were observed away from nests for long periods of time; Dittami et al. (1977) observed Barnacle Geese off nests for 5.2% of the time (73 min/day); and Ryder (1967) noted frequent breaks from incubation in Ross' Geese. However, these authors did not contrast time off the nest during different stages of incubation. Scott (1977) observed female Whistling Swans (*Cygnus columbianus*) spent increasing amounts of time off the nest through incubation as did Afton (1980) for Northern Shovelers (*Anas clypcata*).

Incubation constancy was high during the last 24 to 48 hours of incubation, as hatching of eggs ensued. Although not measured, glycogen stores may have been critical in providing the metabolic energy needed to maintain such high attentiveness at a critical time. Typically, glycogen stores in the vertebrate liver are rapidly depleted during the first 24 hours of fasting (Ruderman et al 1976, Sturkie 1965), such as might occur at initiation of incubation. Subsequently, however, as the fast continues over many days and gluconeogenesis begins to provide glucose necessary for metabolism, glycogen stores are partially replenished in muscles and the liver. The roles of these stores when lipids are depleted during mid to late incubation, during periods of inclement weathern when the geese cannot leave the nest, and at hatching are unknown and deserve attention from researchers. Since replenished glycogen and glucose levels are derived from proteins and lipids during extended fasts via gluconeogenesis (Hanson and Mehlman 1976) measurement of protein and lipid content addresses the major energy sources. Any carbohydrate intake during extended fasts would directly ease protein catabolism and contribute to glycogen stores and glucose levels.

Feeding and Availability of Food

I believe increased time off the nest in Dusky Geese and other waterfowl reflected an elevated need for high dietary intake of energy due to severely depleted energy stores by roughly two thirds of the way through incubation. Sherry et al. (1980) experimenting with incubating Burmese Red Junglefowl (*Gallus gallus*), concluded that the importance of food as a source of energy increased during incubation, and that inattentiveness increased as the length of food deprivation increased. They further noted that if the rate of weight loss was higher than normal, Junglefowl demonstrated a feeding response until returning to a control weight, whereupon they regained their usual condition of anorexia and high attentiveness to eggs.

Not only do geese spend more time off nests but there is also some evidence that time spent feeding during late incubation also increases. Captive Canada Geese spent increasing amounts of time feeding as incubation proceeded (Aldrich and Raveling 1982). Inglis (1977) noted Pink-footed Geese increased time spent feeding from 0 to 2.5% during the last eight days of incubation. Ankney (1977) collected Lesser Snow Goose females during early and late incubation, and found the percent of birds with one half full to full intestines increased from 9% to 29%, respectively, reflecting a rise in feeding activity. Female Whistling Swans increased the proportion of recess time they spent feeding from 77.8% in early incubation to 100% by late incubation (Scott 1977). The proportion of time spent feeding by incubating Shovelers increased throughout incubation (Afton 1979). Cooper (1978) observed Giant Canada Geese fed during 38% of recess time, but noted no apparent increase through incubation. Brakhage (1965) noted Canada Geese fed "ravenously" for a few minutes during each of their 15 minute recesses. Ross' Geese took frequent breaks from incubation and stayed on territory to feed (Ryder 1967). Krapu (1981) observed two Mallard hens that fed 38% of their average daily 2.6 h recess times.

Dusky Canada Geese that eventually abandoned nests spent increasing amounts of time off the nest during the first 13 days of incubation. Perhaps this decreased attentiveness was due to depleted endogenous reserves, which suggests sufficient reserves had not been retained during egg laying (see Aldrich and Raveling 1983). Since food was not at peak availability, time off the nest during early incubation might not be used very efficiently, compared to time off during late incubation.

Availability of food was generally high for incubating geese by mid to late incubation, presumably allowing geese to make increasingly efficient use of their time off the nest. High availability of food existed for Dusky Geese by mid-incubation during the three phenologically early seasons of this study. Food was abundant for White-fronted Geese, Lesser Snow Geese and Brant by mid-incubation (Barry 1967). Ankney (1977b) noticed fresh vegetation growing in territories of Lesser Snow Geese during late incubation, and Harvey (1971) observed that new vegetation appeared by mid June (early to mid-incubation) on Lesser Snow Goose nesting grounds. Widespread new growth of food occurred on nesting grounds of small Canada Geese (B. c. hutchinsii) at McConnel River, Northwest Territories about 10 days before the hatch of goslings (MacInnes et al. 1974). Cooper's (1978) observation that green vegetation hid Giant Canada Geese nests by late incubation probably indicates that food was readily available by late incubation. Thus, food was readily available to geese at the time when stored energy reserves were becoming depleted. I suggest that geese were able to make efficient use of time off the nest, especially during late incubation, by taking advantage of this increasingly abundant exogenous energy source.

The Energy Cost of Incubation

Two conditions developed throughout incubation that contributed to a decline in the energy needs during incubation. These conditions were an increase in average ambient temperatures (Table 17, Drent 1973, Kendeigh 1973) and heat production by the embryo typical of precocial species (Drent 1967, Kendeigh 1973).

Ambient temperatures affected the cost of incubation in two ways. Heat production of birds is higher at lower ambient temperatures than at high temperatures (Drent 1973). The thermal neutral zone for Interior Canada Geese is 12°C to 34°C (Williams 1965). Assuming this zone was similar for Dusky Geese, average mean maximum temperatures were below the thermal neutral zone during early incubation, and within the zone during late incubation. Dusky Geese, and presumably all geese, thus experienced a reduction in energy needs during late incubation.

Ambient temperature also affects the energy requirements during incubation through the cooling and rewarming rate of eggs during and after incubation recesses. Drent (1973) has described the rapid loss of heat from exposed eggs and the relatively long recovery period required to rewarm the eggs upon the return of the parent. Therefore, a recess costs in time and energy by the extra amounts needed to rewarm eggs, and possibly by the embryonic mortality due to chilling that may be associated with long recesses. Siegfried et al. (1976a) examined this relationship in Ruddy (*Oxyura jamaicensis*) and Maccoa Ducks (*O. maccoa*) and found that the ratio of time lost to time exposed declined rapidly as ambient temperatures increased. Thus, applying this relationship to geese, it was more energetically conservative for geese to postpone an elevation in the frequency and duration of recesses to as late as possible in the incubation period, as observed during this study and by Aldrich and Raveling (1983). Aldrich and Raveling (1983) suggested the length of recesses may have evolved to minimize the amount of energy needed to rewarm eggs to their former incubation temperatures. Although Dusky Canada Geese that eventually abandoned nests differed from successful geese in constancy of incubation and frequency of recesses, they did not increase the length of recesses. A strong adherence to this characteristic in both groups of geese supports Aldrich and Raveling's (1983) suggestion.

Heat production by the developing embryos of precocial birds contributes increasingly to the heat energy required to maintain an incubation temperature. Drent (1970) observed that less than 20% of the energy cost of incubation by Herring Gulls (*Larus argentatus*) was derived from the embryo at Day 20, but that about 75% of the energy cost was contributed by the embryo at hatching (Day 30 of incubation). Although, due to the synergistic relationship between the adult contribution and that of the embryo, heat production by the embryo does not significantly affect the cooling rate of eggs (Drent 1973), it does decrease energy demands on the parent during late incubation. Ricklefs (1974) has noted that, ecologically, energy and time are synonymous. Thus, incubating geese experienced a lower energy cost of incubation due to production of heat by embryos, as well as to higher average ambient temperatures in late incubation when energy reserves were considerably reduced.

The total energy cost of incubation of eggs is unknown. If it is small the energy savings discussed above for contributions by the embryo may be insignificant. King (1973) provided a review of the differing thoughts on the energy costs of incubation of eggs.

If environmental conditions (availability of food, ambient temperature) were not as favourable as during this study, geese may still have had the capability of continuing the high constancy of incubation observed if they were able to catabolize more endogenous lipids and proteins than was observed (Part I). This possibility is worthy of further investigation.

Timing of Nesting

Drent and Daan (1980:246) concluded that:

> "the adjustability of laying date, clutch size and pattern of egg care...implies a succession of decisions allowing an adjustment of parental effort to achieve a close fit between parental capacity and environmental opportunity".

Proximate factors involved in the adjustability of laying date for northern nesting geese were suggested by Barry (1962), Raveling (1978), Ebbinge et al. (in Drent and Daan 1980) and others. The phenomenon of synchronous nesting by geese resulting in the timing of hatching coinciding with abundant food has been widely recognized (Barry 1962, Murton and Kear 1973), and related to proximate factors influencing annual variation in timing of nesting. Harvey (1971) concluded that the timing of nesting was regulated to provide maximum food supplies at hatching of the clutch. I believe an important ultimate factor in the evolution of the timing of nesting in geese was the need for an energy source present in optimal amounts during mid to late incubation when stored energy reserves were depleted and environmental conditions allowed geese to spend some time off eggs with relatively minimal extra costs. Because cost of incubation and maintenance was also declining at this time, as the embryo began contributing significant amounts of heat and ambient temperatures ameliorated, the amount of energy needed was further reduced. The lower amount then required for incubation and maintenance could be efficiently acquired from the environment.

Given that timing of nesting has evolved in response to availability of optimal food sources during mid to late incubation then hatching would occur when high quality food was abundant. Ankney and MacInnes (1978) observed that Lesser Snow Geese began incubation with the same amount of energy reserves, regardless of clutch size. If some individual geese had low foraging efficiencies (e.g. see Spurr and Milne 1976, Drent and Daan 1980), it might be best for them to delay initiation of nesting a few days, thus experiencing higher food availability earlier in the incubation period. Other conditions existed, however, that probably did not allow this tendency to favour delays of more than a few days. These conditions included a rapid decline in forage quality (particularly content and concentration of protein) from relatively early in the season (early brooding period) on (Fridriksson 1960 in Murton and Kear 1973, Chapin et al. 1975, 1980), and the shortness of the northern season for growth and preparation for fall migration (Cooch 1961, Barry 1962, Ryder 1967). Predation likely increased as the season progressed as young of predators were produced, elevating the food requirements of the predators.

Individual geese with highly efficient foraging capabilities or better opportunities for foraging (or experienced geese, see Raveling and Aldrich 1983 and Raveling 1981) would be expected to nest earlier as they would be able to meet energy demands at lower availability of food when their reserves became depleted. Initiation of nesting too early in the season would be selected against by factors such as low food availability when reserves became depleted during incubation, predation of eggs concentrated on nests in a patchy snow free habitat (Byrkjedal 1980) or low availability of high protein foods during prelaying and egg laying (Part I of this study). A delay in the hatching date of eggs would cause goslings to encounter lower food quality than they would have had hatching occurred earlier.

Implications to Clutch Size

Winkler and Walters (1983) have recently reviewed published accounts of factors affecting clutch size in precocial birds. The two major themes identified were the "Egg Formation Ability" hypothesis where gametic effort limits clutch size through direct environmental effects, and the "Parental Behaviour" hypothesis wherein clutch size is limited by the costs and benefits of parental behaviour. I believe that the evolution of the timing of nesting to coincide with high availability of food and conditions which allow use of this food at mid-incubation has influenced evolution of clutch size in geese. Previously, I discussed protein availability as a proximate factor limiting clutch size (the first hypothesis above). I suggest here that one ultimate factor has been the need to retain sufficient energy reserves to promote maximum attentiveness to eggs during early and mid-incubation when conditions affecting survival of eggs during the absence of the female are most severe (the second hypothesis above).

Ryder (1970) expressed a similar conclusion but with the major assumption that geese were independent of food during egg laying and throughout incubation. If in fact geese depended on food at (1) prelaying for protein (Part I of this study) and at (2) mid to late incubation rather than at hatching, sufficient reserves would be available for production of an additional one or two eggs. Natural selection would promote those genotypes which utilized this potential, over those that failed to do so. Similarly, those that channeled too large a proportion of endogenous reserves into eggs would have insufficient stored energy to devote maximum energy to nearly constant incubation until food supplies became optional for significant use during recesses. The cost of laying an egg includes (1) the cost of gathering energy and nutrients to put into the egg, (2) energy content of the egg itself, and (3) the time (ecologically equivalent to energy) required for accumulation of the materials and formation of the egg. Thus geese with clutches "too large" would be similarly selected against.

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