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Pre-incubation feeding activities and energy budgets of Snow Geese: can food on the breeding grounds influence fecundity?

Abstract The potential contribution of early spring feeding conditions in the Arctic to clutch size variation was examined in a population of Lesser Snow Geese *Anser caerulescens caerulescens*. Behavioural observations were combined with energetic analyses of food material to derive an estimate of the energy budgets of pre-laying and laying females. Food intake of females between arrival on the breeding grounds and incubation was considerable; estimated energy gains in this period were in the same magnitude as the cost of one or several eggs. The pre-laying period spent on the breeding grounds can thus be energetically beneficial rather than costly. Accumulation of resources for reproduction in Snow Geese is a continual process including the breeding grounds, and nutrient limitation after arrival in the Arctic cannot sufficiently explain the environmental component of clutch size variation. The timing of migration and follicle development is such that clutch size decisions are sometimes made during the late stages of migration and sometimes after arrival. In the latter case food conditions on the breeding grounds may greatly influence clutch size; in the former case they may still influence readjustments of clutch size after the initial decision. The universal negative correlation between clutch size and laying date in Snow Geese can be explained by negative fitness consequences of late hatching, which outweigh the benefits of delayed laying and further nutrient accumulation. Food shortage on the breeding grounds may sometimes be a secondary factor contributing to seasonal clutch size decline.

Key words Clutch size · Feeding ecology · Energy budgets · Pre-breeding period · *Anser caerulescens caerulescens*

Introduction

In birds, particularly herbivorous birds, females face a nutritional bottleneck during egg-laying and incubation (Drent and Prins 1987). This bottleneck appears to be particularly serious in Arctic-breeding geese: in order to match the demand of their offspring during brood-rearing with the peak of spring vegetative growth, parents are forced to initiate breeding at a time of year when Arctic habitats are still quite unfavourable. Only weeks later, after incubation is completed, can females benefit from abundant food to replenish their body reserves. As a result, clutch size in Arctic geese has been considered to be limited by the amount of female body reserves on arrival (i.e. resources imported from the wintering and staging areas), which are further diminished the longer egg-laying is delayed by snow cover of the breeding habitat (Barry 1962; Ryder 1970). After laying, sufficient reserves must be retained to sustain the incubating female until all goslings are hatched.

The concept that clutch size is limited by body reserves was supported by the study of Ankney and MacInnes (1978), who collected Lesser Snow Geese *Anser caerulescens caerulescens* at various stages of the breeding cycle and showed that, on average, heavier arriving females had larger potential clutches (i.e. more developing follicles) and, after laying, females with different clutch sizes did not differ on average in the amount of their body reserves. Because of the apparent lack of feeding opportunity on the breeding grounds before incubation, researchers have emphasized the important role that reserve build-up during spring staging plays for reproductive success in Arctic-breeding geese (Newton 1977; Ebbinge et al. 1982; Thomas 1983; Drent and Prins 1987).

However, the exclusive reliance on "imported" resources is not true for all species of Arctic-breeding

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geese. Brant *Branta bernicla*, for example, can spend an extended period of time on the breeding grounds before initiation, during which they feed heavily (Ankney 1984). Raveling (1978) suggested a fundamental difference in timing of arrival and nest initiation between structurally small and structurally large goose species. According to his theory, small geese, such as Brant, are physically unable to migrate and carry reserves that would sustain them through laying and incubation; they therefore need more time on the breeding grounds for topping-up feeding and egg formation. In contrast, large species, such as Snow Geese, can, according to Raveling, carry sufficient reserves with them and start nesting almost immediately after arrival, development of eggs having already begun during migration.

Observations during the pre-laying time in several "large" goose species do not support Raveling's theory, nor do they support the notion that those geese starve until they start to lay. For instance, pre-laying times of 12–18 days have been reported for Greater Snow Geese *Anser caerulescens atlantica* (Gauthier and Tardif 1991), White-fronted Geese *Anser albifrons* (Ely and Raveling 1984) and Dusky Canada Geese *Branta canadensis occidentalis* (Bromley and Jarvis 1993) in years when nest site availability was not restricted by snow cover. The main activity of females during this time was feeding. Krapu and Reinecke (1992: Table 1.2) present an overview of observations of pre-nesting feeding in geese; all species for which observations were available had been seen feeding, regardless of their structural size.

If extensive pre-nesting feeding does occur in Arctic geese, food conditions on breeding grounds can potentially have an impact on clutch size. However, early spring food in the Arctic is generally considered to be sparse and of low quality, and the actual gains of geese may therefore be negligible; quantitative studies of energy budgets of geese during this period are lacking. Moreover, reproductive decisions – when to start laying, how many eggs to lay – may already be made prior to arrival on the breeding grounds. For the assessment of the potential impact that local food sources on the Arctic breeding grounds can have on goose fecundity, two questions therefore have to be addressed. Firstly, is food availability on the breeding grounds prior to incubation sufficient to make a significant contribution to the females' resource budget? Secondly, where and when are reproductive decisions made, and to what extent can conditions on the breeding grounds lead to changes in these decisions?

In the present study, we investigate these questions for the Lesser Snow Goose (a "large" goose). To address the first question, we estimate energy intake of female geese during the time period between arrival on the breeding grounds and completion of the clutch, combining field data on feeding behaviour and food intake rates with laboratory analyses of energetic content of food material. Time-activity budgets provide an estimate of energy expenditure during the same period, and as a result we can estimate an overall energy budget for pre-incubating Lesser Snow Geese. Regarding the second question, we summarize and discuss available information about the timing of the egg-formation process in Snow Geese in relation to the timing of migratory movements.

Material and methods

Location and habitat

The present study was part of a long-term, comprehensive investigation of Lesser Snow Goose breeding biology at the La Pérouse Bay (LPB) Snow Goose colony. LPB is a shallow bay on the west coast of Hudson Bay (58°4′ N, 94°4′ W), between the town of Churchill, Manitoba, and Cape Churchill. Snow Goose nesting habitat along the shores of the bay is immediately adjacent to extensive saltmarshes that are used during the brood-rearing period. Predominant food plants for Snow Geese on the saltmarsh are goose grass *Puccinellia phryganodes* and the sedge *Carex subspathacea*; these two species also occur in patches in the low-lying parts of the nesting habitat. Nesting areas are dominated by low willows *Salix brachycarpa* and lyme grass *Elymus arenarius* interspersed with short grass *Calamagrostis spp.* and *Festuca rubra*. For a more detailed description of vegetation and habitat see Jefferies et al. (1979) and Cooke et al. (1995).

Snow Goose feeding techniques

In spring, prior to nest initiation and before the growing period of food plants has begun, extensive "grubbing" occurs on the LPB saltmarshes and in the nesting areas. Grubbing Snow Geese remove the top layer of soil (ca. 1–1.5 cm deep) including roots and rhizomes of grasses and sedges and the short above-ground vegetation. These soil-plant clumps are rinsed in the nearest available water to eliminate most of the inorganic soil material, and the remaining plant parts are swallowed. This feeding technique – complete removal of the marsh vegetation – results in patches of bare mud, which are subject to erosion (Kerbes et al. 1990). Both LPB breeding geese and staging geese from colonies further north contribute to grubbing in LPB; it has been unclear to what extent local breeders benefit from food intake by grubbing. Later in the season, when plant growth has begun, geese switch their feeding technique to grazing of the short sward of saltmarsh grasses and sedges. Aside from grubbing and grazing a third feeding method, especially employed in early spring, is shoot pulling, whereby whole plants, mainly *Senecio congestus*, *Elymus arenarius* and *Carex aquatilis*, are pulled out of the ground and their basal parts (storage parts rich in carbohydrates) are selectively eaten by the geese.

General seasonal parameters

Field work for the present study was carried out in May and June of the years 1991–1993, from arrival of geese in LPB until the onset of incubation. Data on daily maximum and minimum temperatures for the time period 1 May–15 June were obtained from the Churchill Weather Office (ca. 30 km west of LPB). Snow cover was evaluated at the time of arrival of the research crew (beginning of May). Peak arrival dates of Snow Goose flocks in LPB were recorded annually. First and mean nest initiation dates and mean clutch sizes were determined annually by standard LPB nest searching procedures (Cooke et al. 1985).

Observations of behaviour

Behavioural observations were made from small wooden observation hides that were located on the east coast of LPB. Hides were placed in a part of the nesting area that allowed full view of the adjacent saltmarsh flats.

During the pre-laying period (before birds had established nest sites on the colony), observations were carried out on any females that were clearly visible from the hides; among those, the focal birds were selected randomly with respect to their present activity. Prior to laying birds move frequently, and it can be assumed that no bird was observed more than once. During laying, observations were focussed on females nesting around the hides. About half of the birds were individually marked with coded legbands; in the unmarked birds, the colour phase (blue or white) of both partners of the pair was used to identify the female while off the nest. Nests were checked regularly to determine the onset of incubation.

Behaviour of female Lesser Snow Geese was observed by instantaneous sampling of focal birds (Altmann 1974; Tyler 1979); birds were observed for 15 min and behaviour was recorded at 20-sec intervals. Focal birds were sexed by comparing the abdominal profiles of both members of a pair, pre-laying and laying females having a more sagging abdomen than males. Categories of behaviour were: FEEDING (in 1992 and 1993 differentiated into GRUBBING, GRAZING and SHOOT PULLING whenever possible), ALERT behaviour, RESTING (SITTING or STANDING in 1992–93), MOVING (WALKING, RUNNING, SWIMMING or FLYING in 1992–93), PREENING, DRINKING, SOCIAL interactions and NESTING (NEST BUILDING or SITTING ON NEST). Observations that were terminated before the 15 min were over (because birds walked out of sight or flew off) were not used for the determination of activity budgets. Similarly, observations of females whose status (pre-laying or laying) could not be determined with certainty were excluded from activity budgets. In some instances, individual females were observed more than once during laying; the majority of birds, however, were observed for only one 15-min period.

To determine the time females spent on the nest during the laying period, continuous observations of nests were carried out over several hours and times of females leaving from and returning to the nests were recorded (1992–93).

Food intake during grubbing

The amount of material taken in by a goose during grubbing was measured in two ways. For the mapping method, a bird was observed for the full length of a grubbing bout at a particular spot, the time spent grubbing was measured and the freshly grubbed area traced on a transparency after the bird had left, thus yielding surface area grubbed (destroyed) per unit time. For the bite count method, the number of bites per unit time taken by grubbing birds was counted, as was the number of rejected (not swallowed) bites. Single bite size was estimated from individual holes made in the surface by a goose beak to be on average 1.5 cm^2.

Samples of above- and below-ground vegetation including the top layer of soil were taken during the laying and early incubation periods on two occasions in 1993. Sampling was restricted to areas immediately adjacent to freshly grubbed spots. Turves of approximately 10 cm × 10 cm with 1.5 cm depth were brought back to the botanical laboratory at the LPB field camp. One quarter (about 5 cm × 5 cm) of each turf was measured (length and breadth), weighed, dried to constant weight and reweighed, while one half (about 10 cm × 5 cm) was measured, then immersed in water and sieved in a metal kitchen sieve (mesh size about 1 mm), thereby imitating the rinsing process employed by geese during grubbing and eliminating most of the inorganic soil particles. The plant material remaining in the sieve was dried.

Turves and sieved material were ground in a Wiley mill to 20 mesh/inch size. Ground samples were dried at 85°C for 24 h. Ash free dry weight (AFDW) was determined by combustion of samples at 550°C for 4 h. Representative samples were then selected for energy determination in a Parr oxygen bomb calorimeter. All ash and energy analyses were carried out in duplicate. If subsamples differed by more than 5% the samples were excluded from further analyses.

Table 1 Costs of activities as multiples of the basal metabolic rate [after Wooley and Owen (1978), Hüppop (1988), Owen et al. (1992)]

Behaviour	Cost	Behaviour	Cost
Sitting	1.1	Alert	2.1
Sitting on nest	1.1	Social interactions	2.3
Standing	1.6	Nest building	2.3
Walking	2.0	Preening	2.3
Feeding	2.0	Swimming	2.8
Drinking	2.0	Flying	14.0

Energy intake and expenditure

A combination of field and literature data was used to estimate the balance of energy intake and energy expenditure of female Lesser Snow Geese before hatch. Balances were calculated as daily energy intake minus daily energy expenditure.

Calculation of daily energy intake involves:

1. The fraction of time spent feeding before/during laying (*year-specific*) from observational data
2. Intake rates in kJ/hour (*constant*), calculated from calorimetric values of food and intake in area/hour
3. Retained fraction of ingested energy (metabolizable energy, ME) (*constant*), estimated at 0.22 × ingested calories (lowest value from Prop and Vulink 1992; see also Karasov 1990)

Calculation of daily energy expenditure involves:

1. Daily activity budgets before/during laying (*year-specific*)
2. The basal metabolic rate (BMR) (*constant*), calculated from body mass (mean body mass of 2950 g for arriving females from Ankney and MacInnes 1978) to be 716.22 kJ/day (after formula from Lasiewski and Dawson 1967)
3. Factors of energy expenditure for each activity (*constant*, Table 1)
4. Costs of thermoregulation (*year-specific*), calculated from daily minimum and maximum temperatures (obtained from the Churchill Weather Office) and body mass specific rate of heat loss below the lower critical temperature (LCT) (Lefebvre and Raveling 1967), calculation see Owen et al. (1992). LCT of Lesser Snow Geese is assumed to be 0°C (see discussion)
5. Costs of egg production (*constant for each clutch size*), calculated as 1347 kJ/egg for egg mass of 124 g (median fresh egg mass of 22,562 Lesser Snow Goose eggs at LPB, Cooke et al. 1995) after Drobney (1980), Sotherland and Rahn (1987); assuming all egg production takes place in LPB, and not considering costs for growth of reproductive tract.

Spatial components

During observations of laying birds, maximum distances of females from nests were recorded. After hatch in 1992 and 1993, observed nests around hides were mapped onto a 20 m × 20 m grid to determine distances between nests.

Length of the pre-breeding period and variation of initiation dates across years

To assess not only daily, but also total energy balances of pre-incubating females, information is needed about the number of days spent on the breeding grounds prior to laying. The determination of arrival dates of individual birds in LPB is impossible because the wariness of the birds early in the season precludes individual identification of marked birds. To assess the length and variation of the time period spent by birds at LPB before laying, we used dates of peak arrival of birds in the colony and mean initiation dates, which are available for 19 years between 1973 and 1992. Mean initiation dates were determined from daily nest searches (for details of methods see Cooke et al. 1985). Peak arrival dates are based on subjective observations by LPB field workers, and are therefore less precise than mean initiation dates (geese arriving at some distance from the field camp may have been overlooked in some years); they are, however, the best available measure of annual arrival dates of geese in LPB. If more than one peak of arriving birds was recorded, we used the midpoint between the peaks. By using peak/mean rather than earliest data we include a larger sample of birds into the calculation and therefore arrive at a more representative value.

Assessments of environmental conditions (subjective and, in some years, through ground emergence transects) by LPB field workers were used to estimate the amount of habitat available – not covered by snow, ice or melt water – each year at the time of goose arrival. Years were classified as either "open" or "restricted" depending on the amount of open ground available.

Results

Length of the pre-breeding period and variation of initiation dates across years

The time span between peak arrival and mean initiation ranged from 2 to 11.5 days, with an average of 8 days (Table 2). The shorter arrival-initiation time spans in more recent years may be a function of the movement of the LPB colony away from the research camp; with the majority of nest sites now at great distances from Camp, peak arrival has become less obvious. It must be noted that the time spans in Table 2 are approximations of annual mean pre-laying times, and there may be considerable individual variation.

The date of mean initiation varied over 23 days in 20 years of study (19 May to 11 June, Table 2). Pre-laying times, however, varied only by 9.5 days and were not correlated with arrival dates; in years with late mean laying dates birds arrived on the colony later (Table 2). It appears that later mean laying dates are imposed by environmental restrictions (cold temperatures and snow cover of the habitat) in some years, but this does not result in longer periods of time spent "waiting" on the breeding grounds themselves.

There was no significant difference in the length of the pre-laying period between years characterized as "open" or "restricted" when the geese arrived (Table 2). The trend was towards shorter periods in restricted years (however, this may in part be due to sampling bias since restricted conditions were more common in recent years, when peak arrival was more difficult to record). Similarly, the degree of synchrony of nest initiation, expressed in standard deviation of laying dates, did not differ between open and restricted years (Table 2). This means that in open years, birds start nesting as gradually as in restricted years, when there is competition for nest sites that become available more slowly. There are fluctuations in the degree of synchrony across years, but they are unrelated to habitat availability.

Table 2 Comparison of laying synchrony and length of pre-laying times in years with different habitat availability on arrival of geese

Year	Availability on arrival	Laying date		Pre-laying time (days)
		Mean	SD	
73	Open	28.5 May	2.05	11.5
74	Restricted	31.1 May	2.53	9.5
75	Open	25.7 May	2.42	12
76	Open	21.9 May	2.13	10.5
77	Open	19.1 May	2.18	9.5
78	Restricted	4.1 June	2.76	10.75
79	Open	31.6 May	1.62	6
80	Open	18.7 May	2.82	12
81	Restricted	28.2 May	2.10	8
82	Open	21.8 May	2.54	9.5
83	Restricted	11.2 June	1.61	4.5
84	Restricted	30.3 May	3.17	2
85	Restricted	23.9 May	2.81	?*
86	Open	26.1 May	1.62	6
87	Restricted	31.0 May	1.57	6
88	?*	29.9 May	1.86	7
89	Restricted	2.3 June	3.43	9
90	?*	29.1 May	1.59	8
91	Open	24.0 May	1.65	7
92	Restricted	4.4 June	1.44	5
Mean (overall)			2.19	8.09
Mean (open years)			2.12	9.33
Mean (restricted years)			2.38	6.84
Difference			U=45	U=55
(Mann-Whitney U-test)			P=0.691	P=0.066

* No records available

Phenology of the study seasons

General seasonal parameters of the three study years are summarized in Table 3. The seasonal conditions of snow melt and temperatures varied greatly over the course of the study. 1991 was a year of early melt and warm temperatures during nest initiation. 1992 was an extremely late year with persistent cold temperatures until after hatch. 1993 was early insofar as there was very little snow cover at the beginning of the season, and the first half of May was warmer than usual; however, temperatures then dropped and stayed low for an extended period of time, resulting in a prolonged period of nest initiation. Geese arrived in mid-May in 1991 and 1993, but a full 2 weeks later in 1992. Mean initiation date was 11 days earlier and mean clutch size was 0.48 of an egg higher in 1991 than in 1992; nest history data for 1993 are unavailable.

Activities before incubation

Activity budgets of female Lesser Snow Geese before and during laying are summarized in Fig. 1. Only observations of females whose nesting status (pre-laying, laying) was known are included. Preening, drinking and social interactions are summarized as "others".

In all years, feeding was the predominant behaviour (53.1–79.2% depending on year and stage) before laying and during the time spent off nest during laying. The re-

Table 3 Weather data, timing, and breeding parameters of the three study seasons

Year	Snow cover at beginning of May	Mean temperature (°C)			Peak arrival	First initiation	Mean initiation	Observation period	Mean clutch size (±SD)
		1–15 May	16–31 May	1–15 June					
91	Medium	−4.9	4.7	8.8	17 May	19 May	24 May	18–29 May	4.13±0.17
92	High	−5.2	0.8	2.8	30 May	3 June	4 June	4–10 June	3.65±0.09
93	Low	−1.9	0.4	4.6	12? May	14 May	?*	17–29 May	?*

* Data unavailable (standard LPB nest searching procedure was discontinued in 1993)

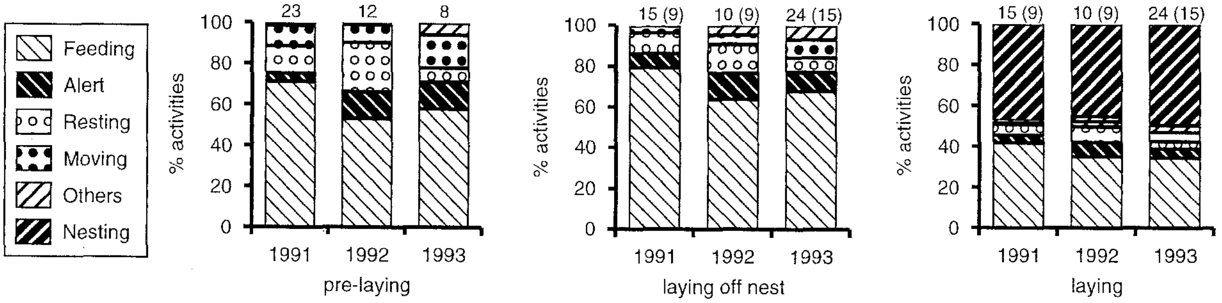

Fig. 1 Activity budgets of female Lesser Snow Geese before and during laying. [*n* (on top of columns) number of 15-min observations, *n* (in brackets) number of observed individual pairs]

Table 4 Mode of feeding of female geese as determined during observation periods of activity budgets (*% known* those observations of feeding behaviour which could be classified as grubbing, grazing, or shoot pulling)

Year	% known	% grubbing of known	*n*
1991*	54.0	70.8	67 15-min observations
1992	39.8	57.3	1657 "feeding" observation points
1993	62.9	88.4	2099 "feeding" observation points

* Only whole 15-min observations classified, not individual observation points

mainder of female off-nest time was divided about equally among alert behaviour, resting and moving; all other activities played a minor role.

During laying, females spent 45–50% of time either sitting on their nests or nest-building, although incubation had not yet started (eggs were cold when checked soon after a female got off the nest). This proportion of time spent on the nest during laying represents an average value for the laying of the whole clutch; time spent on the nest increased as laying progressed, but the small number of observations made at each stage of laying does not allow finer resolution of temporal patterns. Of the time spent off nest, a larger fraction than before nesting was devoted to feeding in all years. The proportion of time spent moving decreased once the nest site was established.

In an inter-year comparison, overall feeding levels were lowest and resting levels were highest in 1992. Alert behaviour was lowest in 1991; so were social interactions (included in "others").

For a detailed analysis of diurnal activity rhythms the data on early morning and late evening parts of the day are insufficient. However, a general evaluation of night-time feeding activity is possible. In 1991, seven 15-min observations were made at "night" (defined as 0.5 h before sunset to 0.5 h after sunrise, but excluding a period of total darkness from 11.15 p.m. to 3.00 a.m., when no observations could be made). There is no significant difference between the fractions of time Snow Geese spent feeding during day and night (Mann-Whitney *U*-test; U=215.5, P=0.682, n=68 and seven 15-min-observations, respectively). In the dark hours of the night, which represent about half of the total night time, geese could not be observed visually but their vocalizations did not change compared to daytime; we therefore assume that feeding and other activities continued during the night. Under this assumption, we can calculate the hours spent feeding per 24-hours for the pre-laying and laying periods of 1991–1993 (Table 6).

Grubbing was the feeding technique predominantly used by females during the pre-incubation period (Table 4). The remaining feeding time was spent grazing. No shoot pulling was recorded during observations of bird activities, although there was some evidence of shoot pulling activity (loose leaves of *Senecio*, the basal parts of which had been removed) in the vicinity of the observed areas. The following calculations of food and energy intake are made under the simplifying assumption that grubbing was the only feeding technique.

Food intake rates

The area grubbed by a single bird in a certain time period was measured on one occasion in 1992, and bites taken per unit time were counted for several birds in 1992 and 1993. More careful observations in 1993 revealed that not all bites taken from the ground are eventually

Table 5 Results of food material analysis (*AFDW* ash free dry weight)

	n	Mean	SD
Fresh turves			
% water	20	82.13	3.06
Dry turves			
% AFDW	20	61.88	8.79
Sieved material			
Dry weight (g/cm^2)	20	0.075	0.018
% AFDW	20	73.17	6.39
Energy (kJ/cm^2)	10	1.213	0.172
Back-calculated energy (kJ/cm^2)*	20	1.063	0.209

* All samples back-calculated from regression of energy content (kJ/g) on % AFDW (r^2=0.958, P=0.0001)

swallowed; the observed rejection rate was 19% of all bites (n=136). Assuming the same rejection rate for 1992, the measured intake rates during grubbing are 740 cm^2 per hour of continuous feeding for the mapping method, 1053 cm^2 per hour for the bite count method, indicating that the estimate of 1.5 cm^2 per single bite may be slightly too high. For all further calculations the conservative estimate of 750 cm^2 per hour of feeding will be used. This corresponds to an intake rate of sieved material of 56 g dry weight per hour of feeding.

Energy content of food material

Results of food material analyses are summarized in Table 5. The higher fraction of organic material in sieved samples versus turves reflects the loss of inorganic soil particles during the rinsing process. Energy content – from the goose's point of view – is only meaningful for sieved material. After the calorimetric analyses of ten samples the energy content of the remaining samples was back-calculated from their AFDW by linear regression.

In further calculations a value of 1.05 kJ/cm^2 (rounded off from 1.063 kJ/cm^2, Table 5) is used. Multiplication with the intake rate of 750 cm^2/h yields an energy intake of 784.5 kJ per hour of feeding and, assuming a digestibility of 22% (see methods), a gain of metabolizable energy of 172.6 kJ per hour of feeding. Although a lot of factors, all of which are prone to errors, are involved in deriving this constant, it is the best estimate of energy intake rate we can arrive at. Consequences of errors in this value will be discussed later.

Table 7 Daily energy balances (in kJ) of female Lesser Snow Geese; costs of egg production not included

	1991	1992	1993
Pre-laying			
Intake	2940.9	2199.5	2205.9
Expenditure	1493.2	1420.8	1559.2
Balance	1447.7	778.6	835.0
Laying			
Intake	1731.4	1449.8	1424.9
Expenditure	1296.4	1292.1	1305.5
Balance	435.1	157.7	119.4

Energy balance

Energy balances of Lesser Snow Geese between arrival in LPB and start of incubation were calculated for 1991–1993. Year-specific factors in the calculation of energy balances and constants involving field data are presented in Table 6 (for other constants see methods). Daily energy balances, not including the costs of egg production, amount to values from +778.6 kJ to +1447.7 kJ pre-laying and from +119.4 kJ to +435.1 kJ during laying (Table 7). Highest daily energy gains occurred in 1991, when daily feeding time and therefore daily energy intake were highest. Values for 1992 and 1993 are similar despite different seasonal phenologies; both timing of melt and timing of arrival differed between those years, resulting in similar conditions being encountered by birds at the time of arrival and pre-laying.

In Fig. 2, calculated balance values for the entire pre-incubation period are presented for a number of different clutch sizes (three, four and five eggs; range of clutch sizes in Lesser Snow Geese is two to six) and a number of pre-laying time spans [1, 5 and 9 days, the egg-laying interval being 1.5 days (Schubert and Cooke 1993)]. For this graphic presentation, it was assumed that all egg production costs are incurred during laying which is in fact incorrect; however, for the net balance after comple-

Table 6 Factors in the calculation of energy balances of female Lesser Snow Geese (see text)

Year-specific factors	1991	1992	1993
Time spent feeding during pre-laying (h/day)	17.1	12.7	13.9
Time spent feeding during laying (h/day)	10.0	8.4	8.3
Thermoregulation costs (kJ/day)	56.9	39.0	38.0
Activity factor* pre-laying	2.01	1.93	2.12
Activity factor* laying	1.73	1.75	1.77
Constants			
Basal metabolic rate (kJ/day)	716.2		
Intake rate (kJ/h of feeding)	784.5		
Digestibility of ingested food	22%		
Costs of egg production (kJ/egg)	1347		

* Multiple of daily BMR, calculated from activity budgets and costs of each activity in Table 1

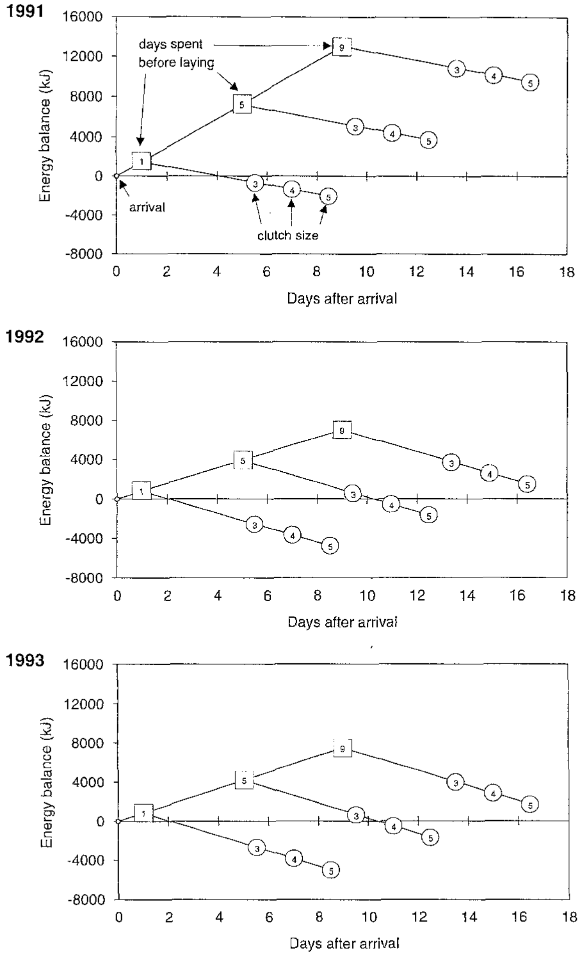

Fig. 2 Energy balances of females between arrival and incubation as calculated from field data on energy intake and expenditure. Starting points (0) are reserves at the time of arrival. *Squares*: balances at onset of laying with different pre-laying times; *circles*: balances at end of laying with different clutch sizes

tion of laying, it is irrelevant when the costs of egg production occur.

Distances from nests

Before laying commenced, most geese were utilizing the saltmarsh areas adjacent to the nesting habitat. Birds gradually moved into the colony over the course of several days and established nest sites.

The distances of laying females from their nests during off-nest periods were recorded on 38 occasions in 1992–1993. In four cases females were out of sight – which may have been far away from the nest or hidden behind vegetation close to the nest. In the remaining 34 cases the maximum distance from the nest was 200 m; 75% of observations were within 30 m. Thus, in the majority of cases in both years, females fed in the immediate surroundings of the nest.

The average distance of a nest to the nearest neighbouring nest in 1992–1993 was 32.4 m ± 14.9 m (no difference between years, t=1.516, P=0.148, n=13, 6). The range of distances to nearest neighbours was 13–60 m. Although exact territory boundaries were not determined, it becomes obvious that most of the time laying females spent off nest was spent closer to their own nest than to nests of neighbours, i.e. in their own territory.

Relative timing of migration and reproductive decisions

Even if net energy balances of pre-breeding Lesser Snow Goose females can be positive, food resources on the breeding grounds may have no influence on fecundity if reproductive decisions are already made prior to arrival on the breeding grounds. To assess where and when clutch size and laying date are determined, we constructed a model of the timing of egg production in the Lesser Snow Goose.

In the process of egg production, the onset of the rapid phase of yolk deposition (RPYD) marks the critical point at which a slowly maturing follicle (of which there are many) turns into one of the current breeding season's potential eggs. RPYD in Lesser Snow Geese lasts about 10 days (Hamann 1983), after which the follicle is ready for ovulation. The duration of RPYD was inferred by Hamann from the number of growth rings in the yolk, which are assumed to be formed at a rate of one per day (Grau 1976). Recent evidence from studies of egg development in wild Ruddy Ducks *Oxyura jamaicensis* suggests that more than one growth ring may be formed per day (Alisauskas and Ankney 1994). However, in the absence of further studies on the duration of RPYD in geese we have to assume that RPYD in each Lesser Snow Goose egg lasts about 10 days. Oviposition is thought to occur approximately 24 h after ovulation (Romanoff and Romanoff 1949), and eggs are laid at intervals of about 1.5 days (Schubert and Cooke 1993).

For Lesser Snow Geese and other Arctic-breeding geese there is evidence that, once all follicles have developed past a certain point, no more follicles can be added to the developing clutch; this has been inferred from observations of follicular hierarchies in dissected birds in which there was a large size gap between follicles undergoing yolk development and smaller, non-developing follicles (Ankney and MacInnes 1978). This pattern is consistent with laying determinacy in Arctic geese (Cooch 1958; Thomas 1988).

From the above information, a time schedule of initiation of RPYD, ovulation and oviposition of each egg can be constructed (Fig. 3). Termination of laying at a certain clutch size (x) can be caused by two mechanisms. The maximum clutch size (n), corresponding to the number of follicles entering RPYD, is set before the first egg is laid by failure to initiate RPYD in follicle (n+1) at time $Ti(n)$ for maximum clutch size of n. Downward adjustment of this maximum can occur later by failure to ovulate the mature follicle (x+1) at time $To(x)$ for clutch size of x.

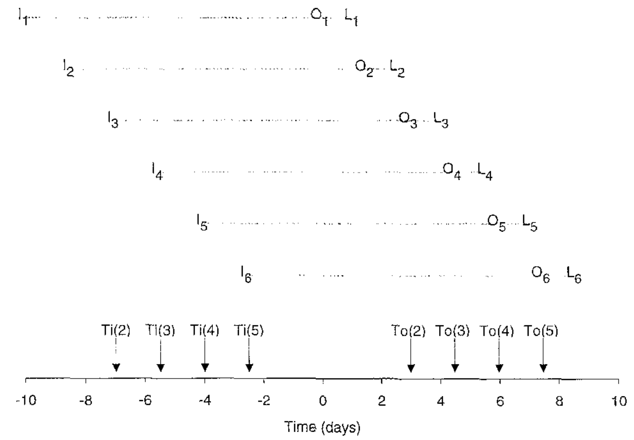

Fig. 3 Timing of egg production and clutch size decisions in clutches of up to six. *Horizontal bars* from top to bottom represent eggs one through six (*I* initiation of rapid phase of yolk deposition (RPYD), *O* ovulation, *L* laying of each egg). Day *0* represents the day of ovulation of first egg, *Ti*(*n*) the decision to terminate maximum clutch size at *n* by failure to initiate RPYD in follicle (*n*+1), *To*(*x*) the decision to terminate clutch size at *x* by failure to ovulate follicle (*x*+1)

If the process of egg formation follows the temporal pattern depicted in Fig. 3, the decision about the laying date of the first egg is made 11 days in advance, at the time when the first follicle enters RPYD. A posteriori modification of this decision may be possible by several mechanisms, the physiological reality of which is largely unknown.

It may be possible for the bird to slow down or speed up RPYD of all follicles, so that laying of the first egg occurs earlier or later. It is unclear whether physiological processes allow flexibility in this point; however, intraspecific variation in the duration of RPYD has been reported in Silver Gulls *Larus novaehollandiae* (Meathrel 1991) and Common Guillemots *Uria aalge* (Hatchwell and Pellatt 1990), which is an indication of at least some potential flexibility.

It may be possible to delay laying by retaining fully mature follicles in the ovary before ovulation. It is unknown whether such a mechanism exists in geese; in seabirds a lag period of up to 11 days between yolk completion and laying has been shown (Astheimer and Grau 1990), but it is unclear if the length of that period can be controlled by the birds. Examination of ovaries of prelaying geese has always shown a size hierarchy of follicles and never more than one follicle of maximum size (Barry 1962; Ankney and MacInnes 1978). This suggests that fully mature follicles cannot be held back without ovulation while the following follicles continue to mature.

If the maturation of a follicle cannot be delayed and has to culminate in either ovulation or atresia, the only way to delay laying, once the first follicle has reached full maturity, is to resorb the follicle. This situation applies in the domestic chicken (Gilbert 1971) and is commonly assumed to be true in wild birds as well (e.g. Murton and Westwood 1977; Newton 1977). Resorption of a follicle immediately before laying means irreversible loss of an egg, since by that time the decision about the potential number of eggs has been made (Fig. 3).

To summarize the information on the timing of reproductive decisions in Lesser Snow Geese: the laying date of the first egg is set approximately 11 days in advance; the potential (maximum) clutch size is set closer to the laying date (2 days before the first egg is laid in a potential six-egg clutch, 8 days before in a potential two-egg clutch; Fig. 3). Once RPYD has begun, it is unclear whether laying date can be modified in any way except by reabsorbing follicles that are ready to ovulate and thus sacrificing potential eggs. After laying has begun, final clutch size may be adjusted downwards by resorption of follicles further down in the follicular hierarchy.

Considering that annual pre-laying time spans in LPB are highly variable with an average of 8 days, there is no clear answer as to where in the migration cycle the process is initiated; the relative timing of arrival and initiation of RPYD appears to vary across years and among individuals within years. It seems that some birds (in some years) arrive at LPB when the process of egg formation is well under way, in which case flexibility of birds to choose both clutch size and laying date according to local environmental conditions is restricted. Other birds (in other years) initiate RPYD after arrival on the breeding grounds and have the potential to adjust clutch size and laying date more freely. If the assumption of one yolk growth ring per day (Grau 1976) is incorrect and the duration of RPYD was overestimated by Hamann (1983), the proportion of birds making reproductive decisions after arrival in LPB will be higher. The general trend is that laying commences sooner after arrival in later years, i.e. in late years reproductive decisions have been made before arrival. This may be necessary because the shortness of Arctic summers sets an absolute limit to the timing of egg-laying – if young hatch too late, they may fail to migrate south before autumn freeze-up (Barry 1962). Wypkema and Ankney (1979) found developing follicles in "some" female Lesser Snow Geese collected before leaving the final staging area at James Bay. Ankney and MacInnes (1978) found large follicles in females collected on arrival at the McConnell River colony, and concluded that clutch size in Arctic geese was set before arrival. However, they did not consider annual variation in the relative timing of arrival and follicle development, and their study was carried out in 2 late years.

Discussion

From data we presented on pre-laying activity budgets of Lesser Snow Goose females, and from data on pre-incubation feeding activity in other goose populations (Krapu and Reinecke 1992), it becomes obvious that the notion of zero food availability for female Arctic-breeding geese between arrival and hatch cannot hold for geese of any structural size. However, feeding time alone does not yield any information about actual pre-incubation energy gains, nor can possible energy gains necessarily be translated into increased fecundity.

Consequently, we have attempted to quantify the amount and energy content of food ingested by Lesser Snow Geese before and during laying, and investigated the potential impact of energy gains during this period on fecundity. The calculation of net energy gain and, subsequently, energy balances, involves a number of estimates and assumptions which have to be critically evaluated.

Translating feeding time into energy budgets

We assumed for the purpose of the calculation that grubbing is the only feeding technique employed by geese before incubation, which is in fact incorrect. However, the assumption that geese only switch to grazing when it is more profitable after the beginning of plant growth seems reasonable; grubbing therefore yields a minimum estimate of food intake. The same is true for feeding selectivity: we assumed no selectivity within the grubbed patches. If geese selectively feed on higher-energy plants (e.g. *Senecio* leaf bases), their energy intake will be higher, and our estimate again represents a minimum.

We measured a food intake rate of 56 g dry weight per hour of feeding. The digestive capacity of a Lesser Snow Goose (amount of food contained in a full gut) was measured by Burton et al. (1979) to be on average 30 g dry weight, which, with a food retention time of about 1.5 h, would correspond to a maximum intake of 20 g dry weight per hour. The rather large discrepancy with the intake rates we measured can be resolved by considering three factors that may differ between Burton's study on wintering geese and our study: (1) even after rinsing of the grubbed material some inorganic soil material still adheres to the food (see ash content in Table 5) and increases specific dry weight. 25% ash content reduces the actual dry biomass ingested from 56 g to 42 g per hour of feeding. (2) Even though pre-nesting geese at LPB feed during a large fraction of time, feeding is not completely continuous, and digestion can take place during non-feeding bouts. For instance, with 75% of total time spent feeding, 42 g dry biomass ingested per hour of pure feeding time translate into 30.5 g dry biomass per hour of total time. (3) Gut morphology in geese is highly plastic, and volume of the intestine can increase twofold in response to diet changes (Burton et al. 1979). Pre-incubating geese in LPB may have a higher digestive capacity than that measured in winter by Burton et al. Even so, our rather crude measurement of surface area grubbed per unit of time may have led to an overestimation of food intake rate.

A number of factors in the calculation of energy budgets were derived from the literature rather than actually measured. In particular, these are BMR as a function of body mass, multiples of BMR for each activity, digestibility of ingested food energy, costs of egg production, and costs of thermoregulation. The magnitude of these factors will have to be assumed correct until more reliable sources for the determination of costs in Lesser Snow Geese become available.

For digestibility, we used the lowest factor reported in any of the examined literature, again taking into account the possible low quality of the food and aiming for a minimum estimate of available energy rather than overestimating it. Gauthier (1993) found in fact that plants consumed by Greater Snow Geese during laying were of high nutritional quality.

We assumed that both intake rates (area grubbed per hour of feeding) and energy content of the food material are constant across years. Both factors were measured in 1992 and 1993 when temperatures before incubation were low compared to 1991; we can therefore assume that average feeding conditions (plant growth and depth of thawed soil available for grubbing) were worse than in warmer years and that we are again factoring in a minimum estimate of food available in other years.

A factor with considerable uncertainty is thermoregulation. Estimates of lower critical temperatures of geese and large ducks vary from –2°C to +14°C (reviewed in Gauthier et al. 1984), and the influence of solar radiation, wind and precipitation on heat loss of birds are complex (e.g. Harvey 1971). A good estimate of thermoregulatory demands on Lesser Snow Geese would only be possible with detailed microclimatic measurements and experimental determination of the thermoneutral zone for the species. Without those, the best estimate is one calculated after the method of Owen et al. (1992), assuming good insulative properties of Snow Goose plumage, and hence a low LCT, as an adaptation to Arctic breeding.

In summary, there is a considerable amount of uncertainty around the absolute values presented in the energy balances in Fig. 2, and they are not necessarily an accurate representation of "reality". Although we tried to derive minimum estimates of energy intake, several sources of error, particularly those concerning food intake rates, may still have led to an overestimation of the actual gains of pre-incubating geese. However, even if real intake rates should be only 75% of the calculated ones, the general pattern of net energy gain before laying still holds, and the notion that pre-laying time on the breeding grounds results in loss of body reserves has to be rejected. Under the assumption that the measured rate of energy intake and the assumed cost of egg production of 1347 kJ/egg are correct, pre-laying female Lesser Snow Geese at LPB have a daily energy surplus equivalent to the costs of producing 0.5–1 egg (Table 7). With an intake rate of 75% of the measured rate, pre-laying geese would still gain the equivalent of the energetic costs of 7–54% of an egg daily. In any case, there is a net gain of energy for every day spent pre-laying, which can potentially be converted into additional body reserves or channelled into egg production.

Our data present only an average magnitude of possible energy gains prior to incubation. The energy balance of an individual bird in a given year will depend on many factors that can be subsumed under the two main aspects of annual and individual variation.

Annual and individual variation in feeding opportunity

Timing of snow melt in Arctic environments, and therefore timing of food availability, vary among years. Quite obviously food intake by arriving geese is impossible as long as there is no open ground. From long term data on Lesser Snow Goose arrival at LPB (Table 2), it appears that arrival is closely correlated with the onset of melt and, as a rule, geese arrive in the colony only after the first patches of ground have melted out. This was certainly true for all three years of our study, which varied greatly in terms of meteorological phenology (Table 3).

After the onset of melt, conditions can be highly variable again. Warm temperatures can favour plant growth and lessen thermoregulatory stress, while cold temperatures, freezing rain et cetera lead to decreased food abundance and quality and increased thermoregulatory costs. Conditions after melt are not necessarily correlated with the timing of melt itself (Table 3: all combinations of early/late and cold/warm are possible). Calculated energy balances between arrival and incubation in an early/cold (1993) and a late/cold (1992) year are virtually identical (Table 7; Fig. 2). However, we do not know where geese stage immediately before they arrive at LPB and what feeding conditions are in those places. It is possible that a costly period of food shortage and waiting for snow melt occurs in late years during the late stages of migration. On arrival at the breeding grounds, average body conditions may therefore vary across years; in White-fronted Geese, body weights on arrival can vary by as much as 500 g among years (Budeau et al. 1991).

In an early/warm year (1991), calculated daily pre-incubation energy gains were about twice as high as in the cold years. Differences among years may be underestimated because we do not have year-specific values for intake rates and energy content of food material. Both may vary among years; variation in food plant quality or biomass may be offset by intake rates or, on the contrary, may be enhanced if, for instance, in a cold year plant biomass is low and there is less opportunity for grubbing because the ground is not sufficiently thawed. In part, these differences are reflected by differences in activity budgets; our data suggest that the relation between food availability and intake rates is a positive one (a higher fraction of time spent feeding in 1991, when warm temperatures allowed plant growth to start earlier), which enhances annual variation.

In LPB, a special feature of annual variation is a long-term decline of food availability due to habitat destruction by the geese themselves. Grubbing has led to severe degradation of both brood-rearing and nesting habitat at LPB (Kerbes et al. 1990; Iacobelli and Jefferies 1991). Vegetated area of saltmarsh has declined by about 12% per year between 1985 and 1992, and in the nesting areas there are bare patches of varying extent. In the remaining vegetated areas, plant biomass has declined by 50% between 1979 and 1991 (Williams et al. 1993a). In the time frame of our study, the ongoing habitat destruction will not have led to noticeable changes in the study area. However, it has to be considered that the present amount of vegetational cover and, possibly, the quality of the remaining vegetation of the grassy parts of the nesting area (which represent the main food source for pre-breeding geese) is already reduced compared to the early days of the LPB colony. Therefore, pre-breeding food intake as we measured it on the east coast of LPB may be lower than in other, non-degraded parts of the colony, or in other colonies. Cooch et al. (1989) showed a long-term decline in fecundity in the LPB geese and suggested that this was a density dependent effect of food shortages after an increase in population size; they did not specify at which stage in the annual cycle the food shortages occur. If, as we suggest below, utilization of local food sources by pre-laying females can have an impact on clutch size, the long-term decline in food abundance in LPB may at least partially explain the concurrent decline in fecundity.

Energy budgets of female geese before incubation depend on several parameters that vary among individuals. The maximum potential food intake before incubation is dependent on the interval between arrival date and laying date, which varies among birds. Arrival date relative to snow melt may also be subject to individual variation, and some birds may arrive before feeding becomes possible; their overall pre-incubation energy balance will be less positive. Clutch size, apart from its direct impact on the energy budget through the costs of each egg, also has a temporal effect: the larger the clutch, the longer the laying period and duration of feeding opportunity. Therefore, the costs of a larger clutch may be partially offset by increased pre-incubation feeding time.

In addition to the temporal parameters, territory quality (in terms of food availability) may differ among individuals. Age and/or breeding experience may work as additional factors, possibly influencing both territory quality and feeding efficiency. Individual differences in food acquisition ability may act year round and lead to differences in body condition that persist from arrival on the breeding grounds until hatch. Physiological parameters such as BMR may also show variation; egg size does so to a large extent (Williams et al. 1993b).

In summary, we do not expect uniform patterns of intake and expenditure among years and among individuals of a population. However, although the extent of topping-up feeding may be highly variable and dependent on individual and seasonal circumstances, the general option to feed and add to imported resources before incubation is open to all individuals.

The negative clutch size/laying date correlation in Arctic geese revisited

Clutch size in Lesser Snow Geese is negatively correlated with laying date both within and among seasons. Although slopes of the decline differ, the pattern is observed every year, regardless of environmental conditions (Cooke et al. 1995). The decline cannot be accounted for by age effects, differential rates of intra-specific nest parasitism, or continuation clutches (Hamann and Cooke 1989). The same negative correlation between clutch size and laying date is common not only among geese, but among birds in general (Klomp 1970).

A proximate explanation for the clutch size/laying date relationship in Arctic-breeding geese was proposed by Barry (1962) for inter-year variation and later extended to intra-year variation (Ryder 1972; Newton 1977). According to this model, geese arrive on the breeding grounds with a finite amount of body reserves which they have to apportion to maintenance on the one hand and reproduction on the other hand. To achieve maximum clutch size, birds must lay as soon as possible after arrival, since any delay will result in increased maintenance costs and thus decreased resources for reproduction, resulting in smaller clutches. If environmental conditions on the breeding grounds force entire populations (in late years) or individual birds (within seasons) to delay laying, clutch sizes decrease. This model, combined for both intra- and inter-seasonal clutch size decline, is referred to as the *nutrient-reallocation model* (Rohwer 1992).

The pre-laying energy gain that we measured for Lesser Snow Geese in LPB, although subject to considerable variation, is in contrast to the nutrient-reallocation model. Instead of losing energy with every day on the breeding grounds before laying, geese gain energy in the pre-laying phase. A delay of initiation is therefore not costly, but profitable in terms of the amount of reserves available for reproduction. Geese that arrive on the breeding grounds with a given amount of body reserves may be faced with several alternative options (provided such options are compatible with the timing and physiology of egg production): lay as many eggs as the imported reserves allow immediately, or spend some time topping up reserves and then lay more eggs. If this is the case, an alternative explanation for the negative clutch size/laying date correlation has to be sought.

A model explaining intra- and inter-seasonal clutch size decline in a wide range of bird species is provided by Drent and Daan (1980). According to their model, individuals accumulating reserves at different speed adjust both clutch size and laying date according to their resources, resulting in the maximum number of surviving offspring. The key point explaining the clutch size/laying date correlation is a relative loss in fitness for each egg associated with later laying date: later hatched young do less well than earlier hatched ones. At a certain point in time in the season, further delay of laying, even though it may allow accumulation of additional resources and result in an extra egg, will reduce the success of all the eggs in the clutch so much that it is not worth it. As a result, the optimal clutch size declines over the season. This model is referred to as the *cost-of-delay model*; it emphasizes the need to optimize both clutch size and laying date in combination.

In several ways, data from the Lesser Snow Geese of LPB point to the cost-of-delay model rather than the nutrient-reallocation model. Nutritional constraints between arrival and incubation are much less severe than previously thought. A cost in terms of fitness loss per egg is associated with later laying dates: goslings hatched later within seasons in LPB had a lower chance of being recruited into the breeding population (Cooke et al. 1984). The pre-breeding period is longer in early years than in late years, and in open years the variance in laying dates is as great as in restricted years; this suggests that later laying dates are not necessarily imposed by the environment, but may be part of an individual optimization process. If the decisions about both laying date and clutch size are made after arrival on the breeding grounds, as it may at least sometimes be the case in LPB (and certainly in Greater Snow Geese, Dusky Canada Geese and White-fronted Geese with extended pre-breeding periods), local environmental conditions will be an important factor in this optimization.

We conclude that the cost-of-delay mechanism is the most likely explanation of the robust pattern of clutch size decline with advancing laying date for Arctic geese, as well as for most other bird species. However, that does not mean that environmentally imposed reallocation of nutrients from reproduction to maintenance has no role at all in determining clutch size in these birds. Because of the large potential for annual and individual variation (as discussed above) it is conceivable that in some cases, such as in extremely unfavourable years, energy balances after arrival may still be negative. In addition, the need to readjust reproductive decisions because environmental circumstances are different from the predicted ones may arise for some birds, regardless of the general environmental characteristics of a particular season. This is underlined by the findings of Hamann et al. (1986), who investigated the relative frequency of follicular atresia in early and late laying Lesser Snow Geese within a season, and in early versus late seasons. No significant difference between the groups was found, and trends were towards more atretic follicles in early layers and early years. Follicular atresia, which can be interpreted as a way to reallocate nutrients, thus does take place, but fails to explain the universal negative correlation between clutch size and laying date.

Relative importance of feeding during spring staging and pre-incubation

In studies of spring fattening in Lesser Snow Geese, daily mass gains range from 12.0–19.3 g, and total mass gain in spring amounts to up to 1160 g (Ankney 1982). If we assume that the pre-laying energy gain we determined for Lesser Snow Geese in LPB was translated into additional body fat at a rate of 44.8 kJ/g [energy content of body fat 39.3 kJ/g (McLean and Tobin 1987), conversion efficiency of fat deposition 88% (Kersten and Piersma 1987)], daily mass gain would be 17.4–32.3 g during the pre-laying time, not considering egg production costs. These values are higher than the ones for spring fattening, which seems counterintuitive. Again, it has to be pointed out that the energy gain we calculated may not be accurate, and the assumed conversion rate into body fat adds further inaccuracy. Moreover, egg production costs are incurred during this period, and net mass gains of pre-laying geese will therefore be lower in any case.

In winter, limited daylight hours are a major factor causing net energy deficits for geese (Owen et al. 1992); on the Arctic breeding grounds, longer daylight hours and prolonged daily feeding times may partly balance lower food quality. At least in the more favourable years, a day's wait on the breeding grounds before laying may thus bring nutritional benefits to a female goose that are equivalent to an additional day of feeding on the southern spring staging grounds.

The important role of resource accumulation on the spring staging grounds is not negated by these findings. Feeding conditions on the staging grounds at lower latitudes will be less subject to annual fluctuations than those on the Arctic breeding grounds, and therefore more predictable and safer to rely on. Moreover, reaching a good condition early on the spring staging grounds may be an advantage during migration if stopover sites have to be reached early before they become depleted by other geese. The advantage of being fat early may persist throughout the breeding season.

In summary, we argue that fecundity in Arctic geese is determined by an interplay of time constraints and different rates of resource acquisition at various times and places, before *and* after arrival on the breeding grounds. Food availability on both spring staging grounds and breeding grounds can contribute to variation in fecundity by determining rates of condition gain at various stages before laying. Local food availability to pre-laying and laying females on or near the breeding colonies should therefore be considered as an additional source of variation in the annual resource budget of geese. Annual variation in fecundity may be brought about by large-scale weather patterns, influencing feeding conditions on migration and after arrival. Individual variation may be caused by small-scale differences in quality of feeding habitat, or by differences among individuals in efficiency of feeding and competing for resources.

The fundamental difference in patterns of resource use between geese of different structural sizes that was suggested by Raveling (1978) cannot be confirmed: while a "large" species like the Snow Goose can accumulate additional resources after arrival on the breeding grounds, there are also "small" geese that start laying immediately after arrival [Spaans et al. (1993) for Dark-bellied Brent Geese *Branta bernicla bernicla*]. In addition to structural size, the distance of migration, location of stopover sites, breeding latitude and local and regional climate conditions will all play a role in determining the patterns of resource accumulation and resource use, and the extent to which local food sources on the breeding grounds can impact fecundity. These patterns will differ not only among species, but also among geographically distinct populations of the same species or subspecies.

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