University of Groningen

Travels in a changing world flexibility and constraints in migration and breeding of the barnacle goose

Eichhorn, Götz

Publication date:
2008

Fuelling reproduction:
differential use of endogenous nutrient reserves
in arctic and temperate-breeding barnacle geese

Götz Eichhorn
Henk P. van der Jeugd
Harro A.J. Meijer
Rudolf H. Drent

Abstract

We compared use of endogenous nutrient reserves in breeding barnacle geese *Branta leucopsis* from traditional arctic colonies in the Barents Sea (BS) and recently established temperate-breeding colonies in the Baltic (BAL) and the Netherlands (NL) by studying clutch and egg size, female body mass (BM) loss and the use of fat and protein stores during incubation. Clutch size increases from North to South from 4 to 5 eggs. Average daily BM loss was almost identical in the two temperate populations amounting to 17.0 and 16.5 g in BAL and NL, respectively, whereas arctic-breeding females from BS reduced the loss significantly to 10.6 g d^{-1}. Temperate breeders initiated incubation with 125 g higher BM than arctic females (1742 g at start of incubation) but after 25 days (the average incubation period for this species) BM was similar among the three populations, averaging 1458 g. Female BM loss until the end of incubation (day 25) amounted to 23% (NL), 22% (BAL) and 15% (BS) of the body weight at the start of incubation. Clutch size, laying date and year showed no significant effect on BM during incubation. By means of deuterium isotope dilution we estimated fat mass (FM) and fat-free mass (FFM) in a sub-sample of females (incubating day 2 to 21) from the NL and BS populations. NL birds had consistently higher fat reserves (65 g on average) than BS birds. However, females from both populations showed a similar rate of FM loss (9.4 g d^{-1}) during incubation. In contrast, FFM was lost at 9.3 g d^{-1} in NL birds but only at a non-significant rate of 1.5 g d^{-1} in BS birds. Accordingly, somatic lipids accounted for 50% and 86% of female BM loss in the NL and BS population, respectively. The respective energy contents of 1 g utilised BM were 21.1 kJ (NL) and 34.9 kJ (BS) which amounts to 376 and 415 kJ d^{-1} drawn from stored energy in NL and BS birds, respectively. Given their level of lipid stores, the higher depletion of somatic protein in temperate-breeding females cannot be caused by energetic demands. Apparently, the temperate birds accept a higher loss of their protein pool perhaps related to relatively delayed moult. The arctic birds face a shorter recovery period before entering moult and must rebuild body stores in preparation for long-distance migration.

Introduction

Evidence for the adaptive significance of somatic nutrient reserves for successful reproduction has been adduced for numerous species of waterfowl (Alisauskas and Ankney 1992a; Afton and Paulus 1992; Arzel et al. 2006). In particular females of arctic-nesting geese, which usually start nesting when local food resources are still scarce, depend on nutrients deposited earlier along the flyway (notably stores of fat and protein) in order to meet requirements for clutch production and incubation (Gauthier et al. 2003; Klaassen et al. 2006b; Schmutz et al. 2006; Drent et al. 2007). Consequently, the amount of nutrient reserves available at laying has been suggested as the primary proximate determinant of clutch size for these birds (Ryder 1970; Ankney and MacInnes 1978; Alisauskas and Ankney 1992a).

In addition to egg production, body reserves are also needed for incubation, and, in some of the northern geese, these stores represent virtually the only energy supply for the female during the entire period (Thompson and Raveling 1987; Spaans et al. 1999; Bolduc and Guillemette 2003). However, female body mass loss during incubation can vary considerably among waterfowl ranging from 3-33% among 24 anatid species with female-only incubation (Afton and Paulus 1992). Furthermore, since females, at the time of egg laying, are unable to predict the breeding conditions they meet later in the reproductive cycle, some reserves have to be retained at the end of laying as a buffer against unpredictable extra nutrient needs (Tombre and Erikstad 1996; Erikstad et al. 1998). Because of these multiple demands, the allocation of body stores to different stages of the reproductive cycle is subject to trade-offs (Gloutney and Clark 1991; Erikstad et al. 1993; Erikstad and Tveraa 1995).

A consequence of insufficient body reserves may be that females, even if not forced to abandon the nest, must take more feeding recesses during incubation (Aldrich and Raveling 1983; Swennen et al. 1993), which can increase the risk of egg predation and increase the length of the incubation period (Aldrich and Raveling 1983; Thompson and Raveling 1987; Tombre and Erikstad 1996). Demands of laying and incubating eggs can affect parental fitness (Monaghan and Nager 1997). Thus, the trade-off between current and future reproduction may be another factor influencing to what extent body stores will be depleted (Stearns 1992; Erikstad et al. 1998). Some studies in which the incubation period was experimentally prolonged did indeed report negative effects on survival and future fecundity (Lessells 1986; but see Tombre and Erikstad 1996; Hanssen et al. 2005).

In order to verify and better understand the different tactics of reproduction evolved in waterfowl, intra-specific studies of nutrient-stores use among populations breeding in different environments are necessary but scarcely conducted so far (Alisauskas and Ankney 1992a; Rohwer 1992; Esler et al. 2001). For example, there is ample reason to speculate that temperate-breeding geese might make other decisions when allocating body reserves to different stages of the breeding cycle than arctic-breeding populations. The amount of body reserves a female has at the start of egg laying is determined by both the amount of reserves she is able to carry from

the staging areas (Ryder 1970; Ankney and MacInnes 1978), as well as by the amount of food available upon her arrival (Prop and de Vries 1993; Choiniere and Gauthier 1995; Ganter and Cooke 1996). Temperate-breeding geese might have an advantage over their arctic counterparts in this respect, since they have both shorter migration routes and experience more favourable conditions upon egg laying. Furthermore, since the breeding season is more prolonged further south, the time to replenish lost reserves is longer in southern populations, which might be a further advantage. Finally, differences in thermoregulatory costs and predation risk between arctic and temperate populations might also contribute to the extent at which body stores will be depleted.

It is our aim to verify such predictions for arctic and temperate-breeding populations of the barnacle goose *Branta leucopsis*. This species established temperate breeding colonies only about 3 decades ago, and the question how a traditionally arctic-breeding species could successfully adopt a temperate breeding strategy during such a short time span is intriguing (see also chapter 6 in this thesis). Here, we compare the amount of body reserves at the start of incubation as well as the rate with which these reserves are depleted during incubation between two temperate and one arctic population. We will show that large differences exist that invite speculation.

Methods

Study populations

Body mass loss was studied in three recently established populations of the barnacle goose, one arctic and two temperate (Fig. 7.1). In the ancestral Barents Sea population (BS), a colony on the northwest coast of Kolokolkova Bay, near the abandoned settlement of Tobseda, Malozemelskaya Tundra, northern Russia (68°35'N, 52°20'E), was studied annually between 2002 and 2006 (Van der Jeugd et al. 2003; Van der Graaf et al. 2004; Eichhorn et al. 2006; chapter 6). Body mass loss was studied during 2003-2005 in this population.

In the Baltic (BAL), birds breeding in the oldest and largest breeding colony situated at Laus holmar (57°17'N; 18°45'E) off the east coast of the island of Gotland, Sweden have been studied from 1984 to 2006 (Larsson et al. 1988; Larsson and Forslund 1994; Larsson et al. 1998; Van der Graaf 2006). Body mass loss was studied in 2000, 2003 and 2004 in this population. In the Netherlands (NL), barnacle geese were studied at Hellegatsplaten (51°42'N, 4°20'E), one of the largest colonies in the Delta area in the southwest of the country (see chapter 6), between 2004 and 2006. This colony consists of several breeding sites, mostly situated on islands. The total number of nests varied between 518 and 537 during the three study years. Body mass loss was studied in 2004 and 2005. Scientific names of species are listed in Table 7.4 or given in the text.
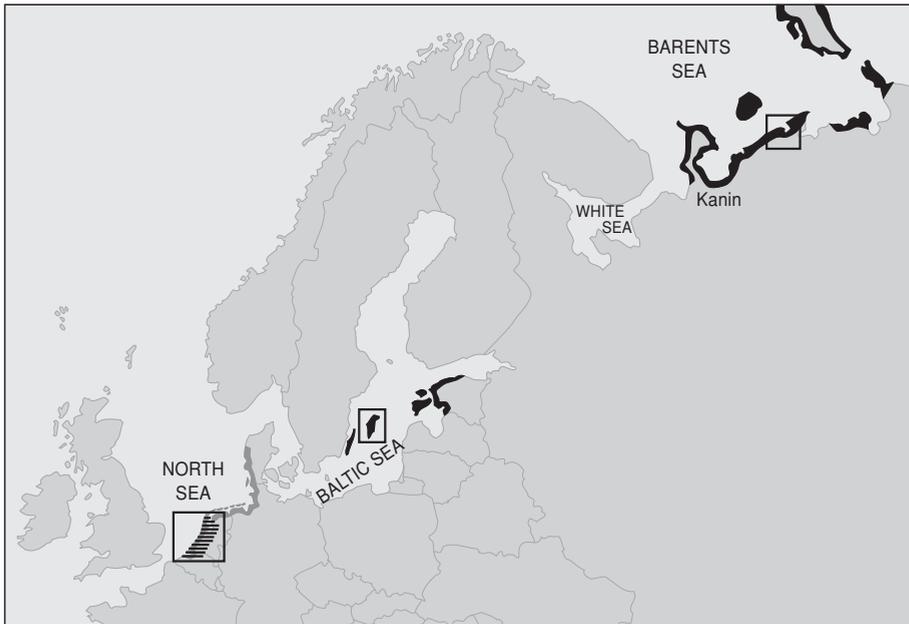
Figure 7.1. Map showing the breeding (in black) and wintering (dark grey) distribution of barnacle geese from the North Sea - Baltic - Barents Sea metapopulation and the location of the three study areas.

Measurements of body mass and reproductive parameters

Body mass of incubating females was measured by inserting a weighing machine (manufactured by T.E.L.L., Germany, type DE6K2) with a platform of 31x31 cm under the nest. This was done by completely removing a turf measuring c. 45 by 45 cm and 10–15 cm deep containing the nest, and placing the scale in the resulting hole. The nest was then carefully put on top of the scale that was fitted with an artificial nestcup (either styrene or wood) glued onto the platform. The remaining part of the scale was then covered by vegetation and soil, taking care that no material would fall into the space between the fixed and moving parts and thereby ensuring that the weight could be recorded accurately. A digital display (linked to the scale by a flexible cable) was placed on a metal standard ca 1 m high at about 5 m from the nest. The display could be read by a telescope from a distance up to ca 200 m. The observer would then retreat to an observation hide or sit concealed on the ground waiting for the female to return to the nest. When females did not return to the nest within one hour the scale was removed and another female was selected. When the female was on the nest the weight of the nest including the female was read from the display. The weight of the nest without the female was recorded

immediately afterwards when the female left the nest of her own accord or when the scale was collected. We attempted to weigh each individual at least twice, during the start and the end of the incubation period. Some females were weighted three times. In addition to using scales, some weights were obtained by trapping females on the nest using a remote-controlled clap net. In the Baltic in 2000 and 2003, all weights were gathered in this way and all females were only weighed once. All birds carried individually recognizable rings fitted to them previously or during nest captures. Body size measurements included tarsus, measured with callipers to the nearest 0.1 mm, and head, measured with a ruler at 1 mm accuracy.

For the data set used to model body mass variation during incubation clutch size was determined during repeated visits to individual nests. In most nests we marked individual eggs and could thus account for partial loss. Additional data on clutch size were taken from the literature as well as from unpublished datasets from the authors and others, including data from other study colonies from the three populations. In these data clutch size was mainly recoded in the second half of the incubation period. Egg length and egg width were measured with a dial calliper to the nearest 0.1 mm in all populations. For the Barents Sea population, additional data on egg length and width were obtained from others. Egg volume was calculated following Larsson and Forslund (1991): volume = 0.4776 x Egg length x (egg width)^2 + 6.462. Mean egg volume in a clutch was calculated as the mean of the estimated sizes of individual eggs. Because all eggs in a clutch were not always measured (e.g., due to predation), total clutch volume was calculated as mean egg volume x clutch size.

Lay date (i.e., when the first egg was laid) was backdated from incomplete clutches found during egg-laying, assuming a laying interval of 33 hrs (Alisauskas and Ankney 1992a). Incubation was assumed to start with the last egg laid for clutches up to 3 eggs, and with the pre-last egg stage for clutches larger than 3 eggs but never later than the 5-egg stage. Clutches of 7 and more eggs are more likely to include dumped eggs. We accounted for egg dumping only if this became apparent during repeated nest visits (i.e., more eggs per interval than expected or additional eggs after clutch completion). Incubation duration in barnacle goose lasts normally 24 to 26 days (Dalhaug et al. 1996; own obs.); data on body mass covered the period day 2 to 25 of incubation.

Estimation of fat and fat-free mass from isotope dilution
We employed deuterium isotope dilution (Speakman et al. 2001) to determine total body water (TBW) contents in a subsample of females from the BS (22 birds in 2003) and NL (20 birds in 2005) populations during day 2 to 21 of incubation. Birds were trapped on the nest, intra-abdominal injected with a 99.9% deuterium isotope solution (Sigma Chemicals) using 1.0 ml insulin syringes, and sampled for blood 90 min later. Birds were kept in cages with no access to food and drinking water during the isotope dilution measurements. Blood was collected from the brachial vein and stored in flame sealed micro-capillaries. An equilibrium time of 90 min was found sufficient to allow for adequate mixing of the marker solution with

the body water pool in the barnacle goose (Eichhorn and Visser 2008). In the field we administered always a dose of 1.0 ml. In the laboratory, having access to an analytical balance (Mettler AG204) and using the same type of syringes, we estimated the average dose mass of 1.0 ml at 1.1153 ± 0.0021 SD g (n=20). To estimate deuterium background levels, blood samples prior to isotope administration were taken from 5 and 4 females from the BS and NL sample, and the respective averages were applied to birds from each study site.

Determinations of δ^2H in blood samples were performed at the Center for Isotope Research, Groningen, see Eichhorn and Visser (2008) for details. In brief, blood samples were prepared by microdistillation in a vacuum line, first heating the broken tubes and then cryogenically trapping the emerging water vapor with liquid nitrogen. Water samples were stored and then automatically injected into a Hekatech High Temperature Pyrolysis unit (Gehre et al. 2004), in which the injected water was reacted with glassy carbon. The resultant H_2 and CO gases, emerging into a continuous He flow through the system, were then led through a GC column to separate the two gases in time and finally fed into a GVI Isoprime Isotope Ratio Mass Spectrometer for the analysis of δ^2H. At least three internal water standards chosen to cover the entire enrichment range of the blood samples were prepared and analysed following the same methods. All sample analyses were run at least in duplicate, more times if values differed by more than 2.5%, and we used the average of values differing from each other by less than 2.5%.

The hydrogen dilution space (TBWd) was calculated by taking into account the quantity of the dose (Q_d, mol), the ^2H concentration of the dose (C_d, atom %), the ^2H background concentration (C_b, atom %), and the ^2H concentration of individual blood samples (C_i, atom %) using following equation: TBWd = $18.02 \cdot Q_d \cdot (C_d-C_i) / (C_i-C_b)$.

TBWd systematically overestimates TBW (by 7.1% in the barnacle goose) and we predicted the latter using the relationship TBW = $96.034 + 0.852 \cdot$ TBWd (r^2 = 0.976, $P < 0.001$), established by Eichhorn and Visser (2008) for the same species. Assuming a water content in the fat-free mass of waterfowl of 66.6% (Eichhorn and Visser 2008), the fat-free mass (FFM) was calculated as: FFM = TBW / 0.666 and fat mass (FM) was subsequently inferred from body mass (BM) as: FM = BM–FFM.

Calculation of energy equivalents

We assumed that the loss of FFM during incubation consisted almost entirely of loss of protein and water, and that the potential loss of other constituents (carbohydrates and minerals) was negligible. We thus equate the loss of dry FFM to protein loss (Groscolas et al. 1991). Physiological energy equivalents of fat and protein were taken at 39.3 kJ g^{-1} and 17.8 kJ g^{-1}, respectively (Schmidt-Nielsen 1997). The energy equivalent for fat tissue was not corrected for water content (as this component is stored nearly free of water) but estimated at 4.5 g^{-1} for wet protein based on an average water content of 75% in the fat-free components of flight, leg and gizzard muscles (Box B).

Estimating daily energy expenditure (DEE)

Resting metabolic rate (RMR, at night, post-absorptive) was determined from oxygen consumption rates in five barnacle geese by Nolet et al. (1992) and in four birds by Stahl et al. (2001) using energy equivalents of 19.7 and 20.1 J ml O_2^{-1}, respectively. Combining data from both studies we detected neither an effect of study nor BM (ranging 1650-2876 g) on RMR. Therefore we apply the mean value of 5.59 ± 0.20 W (± SE, N=9) for further calculations here.

Over the first 22 days of incubation average daily recess time was 177 min for BS females and 80 min for NL birds (see Box C), and we used these values for the calculation of protein and energy budgets during steady incubation. For periods off the nest we assumed an energy expenditure of 1.9 RMR regardless of study population (Afton and Paulus 1992; Stahl et al. 2001). Average temperature during incubation was 12.4°C in the NL colony, and, assuming no costs for thermoregulation, we set energy expenditure while on eggs at 1.0 RMR for these birds. For arctic breeding birds, however, we should account for additive costs for thermoregulation.

Van der Graaf et al. (2001) adjusted the thermoregulation model of Cartar and Morrison (1997) for geese. The authors estimated that under average weather conditions during January to April costs of maintenance metabolism can be subdivided into 52% for basal metabolic needs and 48% for thermoregulation in resting barnacle geese in their wintering area. The average temperature over this period (4.1°C) is comparable with temperatures experienced by incubating geese in the BS colony (4.5°C). However, by choosing a sheltered microhabitat birds can notably save thermoregulation costs (Wiersma and Piersma 1994; Van der Graaf et al. 2001) and the insulated nest itself offers means to achieve such savings (Ar and Sidis 2002). Therefore, we assumed that thermoregulation costs accounted for an elevation of 30% of the maintenance metabolism. Overall, we estimated a DEE of 507 and 743 kJ for NL and BS birds, of which 0% and 28% comprised thermoregulation costs respectively. Energy expenditure while sitting on eggs thus resulted in 1.4 RMR for BS birds. This estimate is close to the 1.5 RMR applied by Afton and Paulus (1992) for geese and slightly lower than 1.7 RMR empirically estimated for seabirds (Tinbergen and Williams 2002).

Statistics

Each bird (individually marked) occurred only in one of the years covered by the data set. For birds with data for more than one season we selected the season with most measurements. If number of measurements was equal among seasons, we made a random selection. To control for differences in structural size between females, we used principal component analysis for the full data set including data from all three populations to combine measurements of tarsus and head length to a single structural size variable, the first principal component (PC1), which explained 85% of the total variance. A second PC1 was calculated for a sub-sample of this data set including measurements of FM and FFM components in BS and NL populations. This PC1 explained 83% of total variance. To account for the strong differences in absolute lay dates among arctic and temperate study populations (Table 7.2),

we computed 'standardized lay dates' as deviations from population-specific annual medians divided by the respective middle 50% range.

We used General Linear Models (GLM) with Tukey post-hoc tests (performed in SPSS 14.0) to analyse differences in clutch and egg size and to compare relevant variables among study populations (Table 7.1 and 7.2). In the analysis of clutch size, mean clutch size per colony and year, weighted for the number of clutches investigated, was used as dependent variable. Assumptions of normality and homogeneity of variances were evaluated using the Kolmogorov-Smirnov test and Levene's test, respectively (Zar 1999). We used a generalized linear mixed model procedure in MLwiN 2.0 (Rasbash et al. 2004) to account for inter-dependency between BM measurements taken on the same individuals during incubation within a given year. Variation of BM was modeled using following explanatory variables: PC1, day of incubation, study population, year, standardized lay date and clutch size (treated as continuous variable). In the subsample including data on FM and FFM each bird was measured only once, and we used ANCOVA in SPSS to test for variation of mass components depending on the explanatory variables: study population (fixed factor) and day of incubation and PC1 as covariates. Final models were derived by backward elimination of possible explanatory variables and their two-way interactions. All results are reported as mean ± 1 standard error (s.e.) and were considered to be significant at $P < 0.05$.

Table 7.1. GLM results investigating variation in clutch size, egg volume and total clutch volume between three populations of barnacle geese *Branta leucopsis*. Apart from differences between populations, mean clutch size differed significantly between years in the North Sea and Baltic populations.

	Clutch size			Egg volume			Clutch volume		
	df	F	*P*	df	F	*P*	df	F	*P*
Population	2,101	10.45	< 0.0001	2,333	3.80	< 0.05	2,333	21.63	< 0.0001
Year	22,101	1.24	0.23	3,333	1.02	0.38	3,333	2.53	0.06
Pop. x year	25,101	1.75	< 0.05	2,332	1.43	0.24	2,332	2.14	0.12
Effect of year by population									
North Sea	17,31	3.08	< 0.005						
Baltic	19,68	2.75	< 0.005						
Barents Sea	11,2	6.68	0.14						

Table 7.2. Summary table of data used to model body mass variation of barnacle goose females from three populations (BS = Barents Sea; BAL = Baltic; NL = Netherlands) during incubation. Sample sizes (n_i = measurements; n_j = individuals) for particular years are shown in the upper part of the table. Note that individual birds did not occur in more than one year in the data set. The lower part of the table gives mean ± standard error for relevant co-variables. Data were pooled for all available years and if there were multiple values per bird within season (i.e. body mass and day of incubation) they were first averaged. Last two columns refer to ANOVA results testing for population differences. Tukey post-hoc test results (for $\alpha \leq 0.05$) are denoted by superscript letters.

year	BS		BAL		NL		Total	
	n_i	n_j	n_i	n_j	n_i	n_j	n_i	n_j
2000			14	14			14	14
2003	25	25	4	4			29	29
2004	38	22	73	36	12	7	123	65
2005	27	17			40	28	67	45
Total	90	64	91	54	52	35	233	153

| Parameter	mean ± s.e.	mean ± s.e.	mean ± s.e.	$F_{2,150}$	P
Body mass [g]	1581 ± 18 [a]	1650 ± 23 [a]	1728 ± 27 [b]	10.05	< 0.001
PC1	-0.13 ± 0.11 [a]	-0.32 ± 0.13 [a]	0.89 ± 0.13 [b]	21.48	< 0.001
Day of incubation	14.2 ± 0.6 [a]	11.5 ± 0.7 [b]	12.4 ± 0.9 [ab]	4.24	0.016
Clutch size	4.0 ± 0.1 [a]	4.8 ± 0.1 [b]	5.0 ± 0.2 [b]	12.50	< 0.001
Lay date [April]	72.5 ± 0.6 [a]	26.3 ± 0.6 [b]	23.3 ± 0.9 [c]	1780	< 0.001
Standard. lay date	0.21 ± 0.14 [a]	-0.24 ± 0.09 [b]	0.03 ± 0.10 [ab]	3.76	0.026
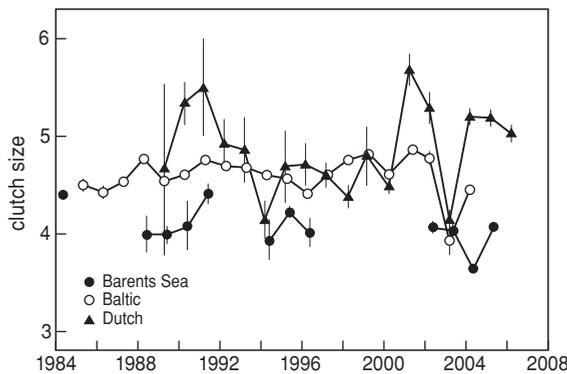
Figure 7.2. Variation in clutch size between the Barents Sea, Baltic and Dutch populations. Each point represents the weighted mean clutch size for that particular year. Data from this study, with additional data for the Arctic population from the literature (Filchagov and Leonovich 1992; Ponomareva 1992; Gurtovaya 1997; Morozov 2001; Kalyakin 2001), and additional data for the Dutch population obtained from unpublished studies (A. van der Heiden, O. Klaassen, R. Kleefstra and P. Meininger pers. comm.).

Results

Clutch size, egg volume and clutch volume

There was considerable variation in clutch size between years and populations (Fig. 7.2; Table 7.1). Clutch size increased from 4.07 ($\pm$0.08) in the Barents Sea population to 4.63 ($\pm$0.06) in the Baltic, and 4.94 in the North Sea population ($\pm$0.10). Differences in mean clutch size between the three populations were highly significant (Table 7.1). In addition, annual variation in clutch size was found to covary in the North Sea and Baltic populations ($R_{pearson}$ = 0.53, n = 16, P < 0.05), but not in the Baltic and Russian ($R_{pearson}$ = 0.29, n = 10, P = 0.4) or North Sea and Russian populations ($R_{pearson}$ = 0.23, n = 10, P = 0.5). The subset of data containing females for which BM loss during incubation was modelled yields a similar pattern of clutch size variation over the study colonies from the three populations (Table 7.2).

In contrast to clutch size, egg volume decreased from 90.62 mm3 ($\pm$0.62) in the Barents Sea population to 88.85 mm^3 ($\pm$0.39) in the Baltic, and 88.30 mm^3 ($\pm$0.72) in the North Sea population. Although differences in egg volume between arctic and temperate populations were significant, they could not counteract the differences in clutch size, and hence total clutch volume still increased significantly from north to south, with total clutch volume being 21% and 11% larger in the North Sea and Baltic populations, respectively, compared to the Barents Sea population (Fig. 7.3; Table 7.1).
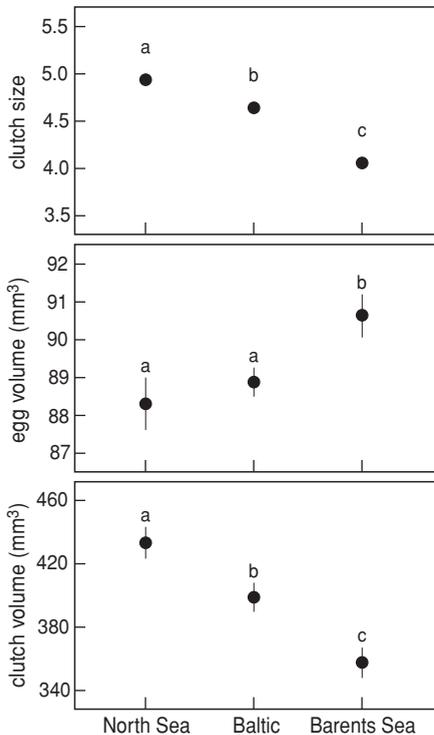

Figure 7.3. Variation in clutch size, egg volume and total clutch volume between the Barents Sea, Baltic and Dutch populations. Letters denote which populations differ significantly from each other.

Body mass

Female BM declined with incubation day (approximately linear) in all three study populations (Fig. 7.4). However, birds from the different populations differed in morphological size (PC1, Table 7.2) and PC1 explained a significant part of the variation in BM. Having accounted for these size dependent differences in BM, the model revealed significant differences in the initial BM and in the daily rate of BM loss during incubation for arctic and temperate females (Table 7.3). Average daily mass loss was almost identical in the two temperate populations in the Netherlands and on Gotland, Sweden, amounting to 17.0 and 16.5 g, respectively. BM loss observed for females incubating in the Russian Arctic was significantly lower at 10.6 g d^{-1}. Temperate breeders initiated incubation with 125 g more body stores than arctic females, which started incubation at 1742 g BM. After 25 days of incubation (the period for this species) BM converged to similar end-points among the three populations averaging 1458 g. Clutch size, (standardised) laying date and year showed no significant effect on incubation mass.

Fat and protein stores

Results of the body composition analyses from isotope dilution in a subsample of incubating females are summarized in Table 7.4 and Fig. 7.5. The pattern for BM (Fig. 7.5 A) resembles the findings from the larger data set, though population-specific differences of BM were not statistically significant in this smaller subsample. FM was significantly lower in arctic compared to temperate (NL) breeders (65 g difference on average, Table 7.4) but decreased at a similar rate of 9.4 g d^{-1} on average in females from both populations over the study period of 20 days (Fig. 7.5 B). In contrast, loss of FFM during this period differed significantly between populations (interaction Day_inc x population in Table 7.4). Temperate breeders depleted FFM at 9.3 g d^{-1}, whereas the estimated loss of 1.5 g d^{-1} for arctic breeders was not significant different from zero change of FFM ($F_{1,21} = 0.27$, $P = 0.61$; Fig. 7.5 C). Accordingly, somatic lipids accounted for 86% and 50% of female BM loss in the BS and NL population, respectively. Thus, compared to their arctic conspecifics, temperate birds started incubation with higher levels of both fat and protein stores, and retained more fat, but less protein, towards the end of incubation (note that in this data set no values were obtained beyond day 21).
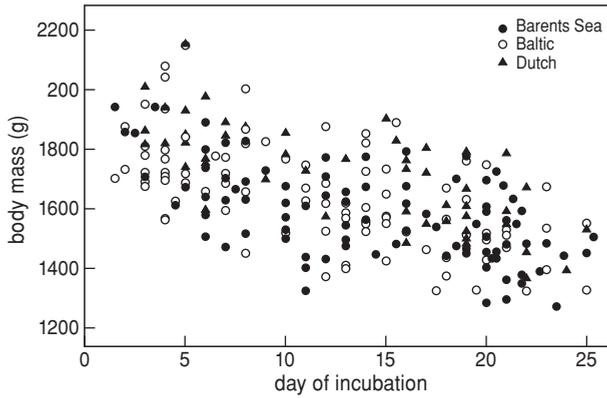
Figure 7.4. Body mass of incubating female barnacle geese. Shown are all 233 individual measurements taken on 153 birds from 3 populations.

Table 7.3. Model summary of body mass loss during incubation (day 2 to 25) of female barnacle geese from three populations (BS = Barents Sea; BAL = Baltic; NL = Netherlands). Parameter estimates are given relative to the BS population. Post-hoc comparisons among populations refer to Wald tests.

Final model		B	s.e.(B)	Df	X^2	P
Intercept		1742	19.9	1		
PC1		81.2	9.7	1	69.7	<0.001
Day_inc		-10.6	1.0	1	104.8	<0.001
Population	BAL	124.4	26.7	2	25.9	<0.001
	NL	125.1	32.5			
Day_inc x population	Day_inc x BAL	-5.9	1.4	2	23.2	<0.001
	Day_inc x NL	-6.4	1.6			
rejected terms						
Year				3	1.15	0.77
Standardised Lay date				1	0.61	0.43
Clutch size				1	0.46	0.50
Post-hoc comparisons of populations						
Population	NL - BAL			1	0.00	1.00
	NL - BS			1	14.80	<0.001
	BAL - BS			1	21.75	<0.001
Day_inc x population	NL - BAL			1	0.12	0.73
	NL - BS			1	15.87	<0.001
	BAL - BS			1	18.37	<0.001

Table 7.4. ANCOVA results of body mass (A), fat mass (B) and fat-free body mass (C) of incubating female barnacle geese. Mass loss during incubation (with day of incubation and PC1 as covariates) was compared for birds from the NL population (n=20) against birds from the BS population (reference category; n=22). Non-significant terms were removed by backward deletion from the model and are in brackets; given is the F-value when included in the final model. Not shown are the parameters clutch size and standardised lay date, which had no significant effect on any of the mass components.

A) Body mass

Parameter	B	s.e.(B)	df	F	P
Intercept	1852	31.3	1	3494	<0.001
PC1	87.0	15.3	1	32.48	<0.001
Day_inc	-14.8	2.3	1	42.62	<0.001
(Population)			1	1.43	0.24
(Day_inc x population)			1	1.55	0.22
Final model (R^2= 0.64)			2	34.25	<0.001
Total			41		

B) Fat mass

Parameter	B	s.e.(B)	df	F	P
Intercept	291.8	18.7	1	352.90	<0.001
(PC1)			1	0.19	0.66
Day_inc	-9.4	1.2	1	57.00	<0.001
Population	65.0	16.6	1	15.33	<0.001
(Day_inc x population)			1	0.40	0.53
Final model (R^2= 0.64)			2	34.84	<0.001
Total			41		

C) Fat-free mass

Parameter	B	s.e.(B)	df	F	P
Intercept	1505	33.3	1	4503	<0.001
PC1	73.6	13.2	1	30.96	<0.001
Day_inc	-1.5	2.3	1	10.77	0.002
Population [a]	48.8	50.9	1	0.92	0.34
Day_inc x population	-7.8	3.4	1	5.29	0.027
Final model (R^2= 0.59)			4	13.30	<0.001
Total			41		

[a] This parameter was retained in the final model (though its main effect was not significant) because of the significant interaction with Day_inc.
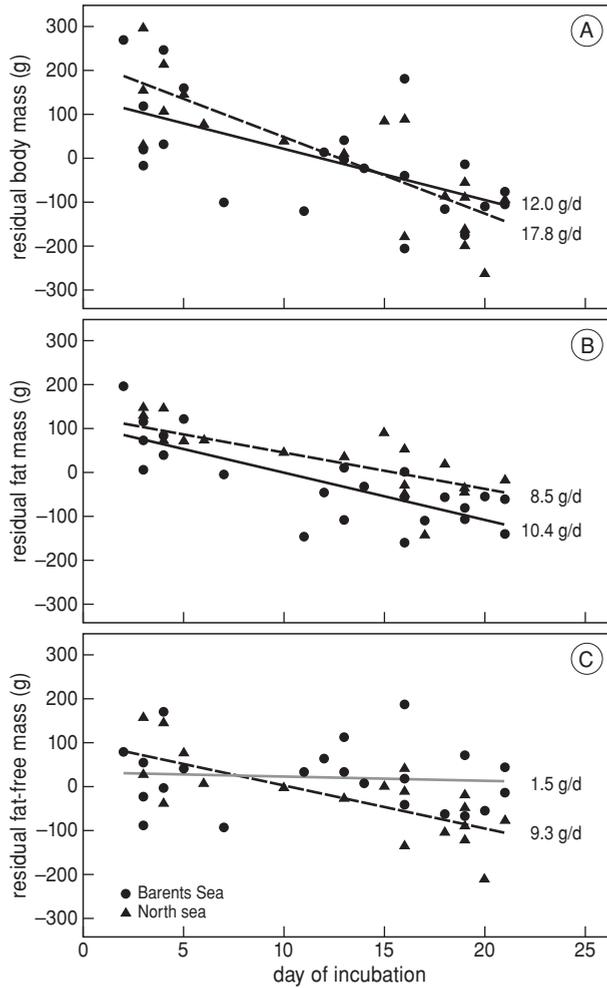
Figure 7.5. Loss of body mass (A), fat mass (B) and fat-free body mass (C) during incubation compared for birds from BS (solid line) and NL (broken line) breeding populations. Mass values represent residuals from a linear regression of mass against PC1. Values shown at the right refer to the estimated slopes of the regression lines, which were significant different from zero (P < 0.05) for all regressions (tested separately for BS and NL birds) except for residual FFM of BS birds (solid grey line).

Discussion

Clutch and egg size

Temperate-breeding birds laid larger clutches compared to arctic-breeding ones, although eggs were of slightly smaller size. In contrast to the pattern observed for most altricial species (Ricklefs 1980), barnacle geese thereby conform to a pattern that has also been found in other waterfowl, including northern-latitude geese (Rohwer 1992; Figuerola and Green 2006). Both somatic nutrient stores and local feeding conditions contribute to the amount of resources potentially available to the laying female and have been suggested as primary proximate determinants of clutch size (Lack 1968; Rohwer 1992; Johnson et al. 1992). Comparison of post- and pre-laying mass of females from both populations in order to infer relative endogenous and exogenous inputs to egg production is revealing. The average pre-laying BM of females in the BS colony was 1970 g (n = 45, 2003 and 2004 pooled, Eichhorn 2005). No direct measure of pre-laying BM is available for temperate breeding geese. However, if we assume similar BM gain rates for Dutch pre-laying geese and Dutch spring staging geese, we can use BM data collected at a staging site in the north of the Netherlands between 18 March and 20 April 2004 (n = 109) to extrapolate a BM of 1999 g for 25 April, the average laying date of NL birds. Because of the assumption that virtually all of the staging birds in this sample belonged to the BS population (based on ring-readings) and the notable differences in structural size (PC1) of BS and NL birds (Table 7.2) and its effect on BM (Table 7.3), we have to correct these pre-laying masses accordingly. When this is done, the estimated BM losses during laying are 2009-1867 = 142 g for 5 eggs (NL) and 1981–1742 = 239 g for 4 eggs (BS). Apparently, the better feeding conditions during egg-laying allow temperate-breeding birds to allocate a higher proportion of locally-obtained resources directly to egg production, whereas arctic-breeding birds have to draw more from body stores at that time of the season. Moreover, arctic nesters have to pay the cost of migration and start breeding with lower body stores compared to temperate birds.

Although of smaller body size than barnacle geese from the NL population, the arctic-breeding BS birds laid larger eggs. Resource limitation for the laying female (increasing with latitude/migratory distance) in combination with egg-size adjustment to a harsh environment (Koskimies and Lahti 1964) may enhance the inverse relationship we found between egg size and clutch size among our three study populations. A trade-off between egg size and number has been shown at the interspecific level for waterfowl, including geese, but has not been found within species of waterfowl (Christians 2000 and references therein).

Body size and body mass

If we want to derive any general conclusions about body size differences between temperate and arctic populations (Table 7.2), we have to take into account that adult body size is related to nutritional conditions during the juvenile growing phase (Larsson and Forslund 1991; Sedinger and Flint 1991). Adult body size of successive cohorts in the Baltic was found to decrease rapidly as a result of

increased competition for food when colonies grew older (Larsson et al. 1998). The Baltic population is currently decreasing in terms of breeding pairs, and the main study colony was over 30 years old when the data we present here were collected. We therefore attribute the small body size of Baltic birds to this competition (or density) effect. However, the BS, and especially NL, populations still enjoy rapid growth, indicating better food conditions for offspring growth in these populations. The difference in body size between these populations might tentatively hint at temperate populations evolving towards a larger body size.

We found marked differences in the rate of BM loss during incubation between arctic- and temperate-breeding barnacle geese, with temperate-breeding females losing up to 60% more mass each day. However, temperate-breeding females initiated incubation with a body mass that was 125 g higher than that of arctic-breeding females. Assuming the rates we found to be constant over the whole incubation period, female BM loss until end of incubation (day 25) amounted to 15% (BS), 22% (BAL) and 23% (NL) of BM at start of incubation. These values are conservative estimates, because few measurements are available for the first and last two days of incubation (see Fig. 7.4) when the rate of mass loss may have been even higher due to changing lipid and protein catabolism, a phenomenon which has been observed in fasting geese (Le Maho et al. 1981; Boismenu et al. 1992).

BM (after laying) was not related to clutch size or (standardised) lay date. Because clutch size decreased with (standardized) laying date ($F_{1,149} = 4.98$, $P = 0.027$, accounting for population effects in the model), BM at pre-laying most likely decreased with laying date. A parallel decline of both pre-laying BM and clutch size would then cause a similar BM after laying. Bêty et al. (2003) showed how greater snow geese might optimise individual egg-laying decisions (when and how many) according to their body condition. That females (of the same population) deplete their body stores during laying to similar levels at clutch completion regardless of clutch size has been observed, for instance, in lesser snow geese, and is clearly adaptive for birds which draw mainly on body stores during incubation (Ankney and MacInnes 1978). Our results indicate that the actual level of a post-laying nutrient reserve threshold was similar among either temperate or arctic-breeding females but was different between populations: temperate breeding geese laid one egg more; nevertheless, they commenced incubation with larger nutrient reserves than geese from the arctic population.

Depletion of protein and energy stores during steady incubation
Almost the entire loss of BM through incubation (day 2 to 21) in arctic-breeding females comprised fat, whereas in temperate females both fat and lean mass contributed equally to the decrease of BM. Energy density of wet lean tissue is considerably lower than that of fat (see methods). The energy contents of 1 g utilised BM were 21.1 kJ in NL birds and 34.9 kJ in BS birds (calculated from the slopes in Fig. 7.5). Consequently, and despite the strong difference in BM loss, energetic yields from body stores differed less between populations, amounting to 376 and 415 kJ d^{-1} in NL and BS birds, respectively.

To look for proximate reasons to explain the differential use of body components in the two study populations we have to consider the budget of nutrient and energy expenditure and uptake. Both lipid and protein depletion depend on energy expenditure. However, the ability to spare proteins during periods of fasting additionally depends on the organism's adiposity (Caloin 2004). Given the consistently higher lipid reserves (and lower energetic costs, see below) in temperate-breeding females, their higher use of somatic protein cannot be caused by energetic demands. Instead, we suggest that the reduced (feeding) recess time of NL birds was insufficient to replace much of their endogenous protein loss. Over the first 22 days of incubation average daily recess time was 177 min for BS females but only 80 min for females from the NL colony (see Box C).

Daily maintenance nitrogen requirements of 0.44 and 0.45 g kg^{-1} have been reported for magpie goose *Anseranas semipalmata* and Cape Barren goose *Cereopsis novaehollandiae* (Dawson et al. 2000; Allen and Hume 2001). Le Maho (1981) measured a daily total endogenous N loss of 0.16 g kg^{-1} in domestic geese during starvation (at start of phase two). Using the average value of these three studies as proxy for barnacle geese of 1660 g BM at mid incubation yields maintenance protein requirements of 3.6 g d^{-1} (assuming a nitrogen fraction in protein of 0.16, Blaxter 1989). This would mean that NL birds, which experienced a net loss of 2.3 g d^{-1} of dry somatic protein (at 75% protein hydration, see methods) could only balance 35% of these requirements during their recess bouts, whereas BS birds apparently gained 90% of their requirements during feeding recesses. Translating the protein input from feeding into nitrogen retention per daily recess time reveals 2.6 (NL) and 2.9 (BS) mg min^{-1}. These values are comparable to the 2-4 mg min^{-1} N retention rates in barnacle and dark-bellied brent geese estimated during the period of intensive protein deposition in spring (Prop and Black 1998; Prop and Spaans 2004). Assuming that BS and NL birds retained similar proportions of ingested N, the similar N retention rates indicate comparable feeding conditions in both breeding habitats. This is consistent with equally high N contents in forage plants collected at both sites (see chapter 6).

Unlike endogenous nitrogen losses, energy expenditure should certainly be lower in temperate-breeding birds, since ambient temperatures were almost always above the lower critical value at which costs for thermoregulation will be induced (Box C). In line with these considerations, daily energy expenditure (DEE) measured during incubation by the DLW technique was about 50% higher in eight species of arctic breeding shorebirds compared to similar sized temperate-breeding birds (Piersma et al. 2003). Also, the higher nest attentiveness of geese from the NL population (Table 7.4) minimized costs for activities (mainly feeding) off the nest. Of the estimated DEE of 507 and 743 kJ (see methods for details) NL and BS birds, respectively, would have balanced 74 and 56% with their body stores. Balancing the remaining costs through feeding would demand an intake rate of 1.6 (NL) and 1.9 kJ (BS) per min off the nest, which seems feasible if compared to average rates of 1.5 to 2.4 kJ min^{-1} found for barnacle geese foraging in different habitats during spring (Prop and Black 1998).

Preliminary energy budgets for the entire incubation period

Assuming the daily rates of depletion of FFM and FM that have been determined for the period day 2 through 21 (Table 7.4, Fig. 7.5) to apply throughout the 25 day incubation period the body stores present at the start and again at hatch can be estimated (see also appendix). For the arctic birds 260 g of the original FM of 292 g would be depleted during incubation, leaving a residue of 32 g at hatch. These figures corroborate the provisional fat budget for Russian birds presented by Drent et al. (2007), where the FM at commencement of incubation was estimated at 310 g (and residue at hatch hence slightly higher than in the present exercise). The FFM of arctic birds declined by only 38 g (of the 1505 g available at commencing incubation 1467 g would remain at hatch). For the non-migratory temperate counterparts (NL) the corresponding estimates are 213 g for FM depletion (body stores declining from 357 g at start to 144 g at hatch) and a loss of 233 g for FFM (1554 g at start, 1321 g at hatch). BM at hatch would converge at 1499 g for arctic birds and 1465 g for temperate breeders, but as noted the composition of the body differs. Although these figures require confirmation by sampling females at hatch, the preliminary calculations support the notion that females in the arctic work to a stringent budget and must supplement their endogenous energy source by feeding throughout incubation to avoid complete depletion of their FM. In this view the time off the nest is adjusted to assure the exogenous energy input needed to balance the budget (see calculations above). Since the temperate breeders commence incubation with higher FM and moreover face lower daily costs they can reduce their daily feeding time compared to their arctic counterparts. Table 7.5 shows that attentiveness during incubation (% time on nest) is consistently higher in barnacle geese incubating in temperate regions (two studies) compared to the arctic birds (two studies) by a margin of 5%. It will be seen from the table that species breeding in the arctic generally achieve incubation attentiveness in the range 88-99.5%. There are only a few previous estimates of the contribution of endogenous stores to total incubation cost and these do not reveal a simple pattern to either body mass (see Thompson and Raveling 1987) or migration distance. Relating species/population means of BM loss to nest attentiveness underlines the importance of incubation recesses for the regulation of endogenous nutrient reserves (Fig. 7.6). Two studies (on emperor and white-fronted goose) 'fall off the line' and may require confirmation.

Alsos et al. (1998) showed that individual barnacle geese females with rich food supplies in their feeding territory achieved higher attentiveness than neighbours with fewer resources, again suggesting that time off to feed is regulated to achieve a given energetic intake. Prop et al. (1984) showed that individual barnacle geese subsequently abandoning incubation spent increasing amounts of time feeding daily, suggesting that these birds were in poor body condition and needed to compensate for this (see also Schmutz et al. 2006). Aldrich and Raveling (1983) studied incubation attentiveness in 13 pairs of captive (and wing-clipped) western Canada geese kept in large flight pens in California. Females were weighed at the onset and thereafter at weekly intervals, and incubation constancy monitored by weighing platforms. Overall attentiveness was 97.5% (and lost 27% of initial body

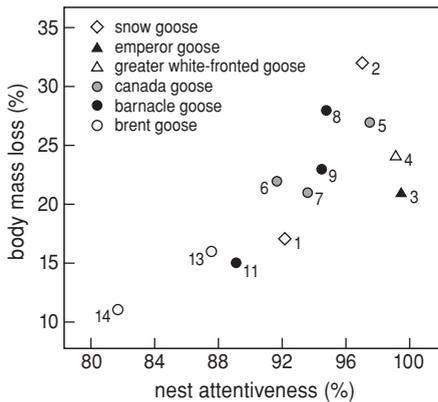**Table 7.5.** Body mass loss and nest attentiveness of northern geese during incubation.

study/species/subspecies/population		g BM at start of incubation	% BM loss	%Time on nest	km from wintering area*	% energy stores to inc.
1) Greater Snow G.	*Anser caerulescens atlanticus*[1]	2590	17	91.4-93	4000	
2) Lesser Snow G.	*Anser c. caerulescens*	2530	32	97.1	3400	78
3) Emperor G.	*Anser canagicus*	2230	21	99.5	1500	
4) Gr. White-fronted G.	*Anser albifrons albifrons*[2]	2635	24.1	99.2	4500	
5) Western Canada G.	*Branta canadensis moffitti*	4300	27	97.5	0	
6) Dusky Canada G.	*Branta c. occidentalis*	3206	22	91.7	2600	58
7) Cackling Canada G.	*Branta c. minima*	1387	21	93.6	3300	39
Barnacle Goose	*Branta leucopsis*					
8)	Great Britain	2020	28	94.8	0	
9)	Netherlands (NL)3	1867	23	94.6	0	74
10)	Baltic (BAL)[3]	1866	22		1000	
11)	Barents Sea (BS)[3]	1742	15	89.1	3200	56
12)	Spitsbergen[4]			89.5-93.2	3000	
13) Dark-bellied Brent	*Branta bernicla bernicla*[5]	1269	16	87.6	4500	52
14) Light-bellied Brent	*B. b. hrota*	1143	11	81.7	3200	17
15) Black Brent	*B. b. nigricans*[6]			89.6		

Data from Afton and Paulus (1992), updated for [1](Reed et al. 1995; Poussart et al. 2001), [2](Spaans et al. 1999), [3](this study; nest attentiveness Box C this thesis), [4](nest attentiveness as 89.5% from Tombre and Erikstad 1996; 93.2% from Tombre et al. unpubl. data for 1997; 89.9% from Alsos et al. 1998), [5](Spaans et al. 2007), [6](Thompson and Raveling 1987). * Breeding location taken from original source; if winter sites were not given therein, taken from Owen (1980).

mass) but the individual data showed that total recess time during incubation was dependent on BM at onset, a relation also evident on a weekly basis. As expected, BM loss between weightings depended on weekly recess time (individuals with shorter feeding times accepting higher losses of body mass). These three studies on individual incubation constancy support the notion that feeding time is adjusted on the short term in relation to state of the body stores.

Factors explaining differences between arctic and temperate populations
We have shown that the composition and dynamics of nutrient reserves used to sustain females through incubation can differ remarkably among high-latitude and temperate breeding barnacle geese. While saving on travel costs and profiting from a relatively higher input of current diet to egg production enabled temperate geese to lay larger clutches and still start incubation with larger nutrient reserves, they make less use of food uptake through incubation and deplete in particular their protein stores more than arctic geese. What may explain these different strategies of nutrient reserve use?

Figure 7.6. Body mass loss during incubation in relation to nest attentiveness. Species of geese are marked by common symbols. Numbers refer to studies presented in Table 7.5.

Barnacle geese from all three populations usually undergo moult on their breeding grounds. Even if nutrient and energy demands of moult may be largely or fully supplied by feeding, moult is unlikely a period of significant nutrient deposition (Hohman et al. 1992). Moreover, BS birds have to prepare for 3,200 km fall migration, whereas NL birds overwinter in or near to their breeding and moulting grounds. Therefore, temperate-breeding females might tolerate higher BM losses during incubation because they have a much longer period of recuperation before entering the moult. The interval between hatching (when nutrient reserves are depleted at its most) and start of moult is ca 35 days in BAL and NL, but only 16 days long in BS (chapter 6). According to this interpretation, arctic-breeding females regulate their daily deposition rate of protein to avoid depletion of their body stores. Arctic birds thus accept longer daily feeding times (Table 7.5). Further work will be needed to quantify other factors in the nest attendance trade-off (including predation risk, protection from egg-dumping, etc.). For a better understanding, we also need to extend our knowledge of body composition to embrace the post-incubation period.

Acknowledgements

Appendix 7.1. Incubation fact sheet for barnacle geese from the Barents Sea (BS) and the Netherlands (NL).

	BS	NL	remark
Before incubation:			
Estimated pre-laying BM (g)	1981	2009	Eichhorn (2005) and extrapolated
BM at start of incubation (g)	1742	1867	full data set on BM
Clutch size	4.07	4.94	
Egg volume (mm^3)	90.62	88.30	
Clutch volume (mm^3)	357.2	432.1	
During incubation:			
Incubation duration (d)	25 (22-26)	25 (22-26)	(Dalhaug et al. 1996; own obs.)
Time off nest per day (min)	177	80	first 22 days of incubation
Daily mass loss BM (g)	10.6	17	full data set on BM
Daily mass loss BM (g)	12	17.8	subsample for body composition
Daily mass loss FM (g)	10.4	8.5	subsample for body composition
Daily mass loss FFM (g)	1.5	9.3	subsample for body composition
Energy budget			
RMR (kJ/d)	483	483	for BM at half way incubation
DEE in RMR units	1.7	1.05	
Estimated DEE (kJ/d)	743	507	
Energy from body (kJ/d)	415	376	
Shortfall (kJ/d)	328	131	
Net intake needed (kJ/min)	1.85	1.64	
Contribution body (%)	56	74	
FM dynamics			
at day 0 (g)	292	357	
Depletion over 25 d (g)	260	213	
at hatch (g)	32	144.5	Day 25 of incubation
FFM dynamics			
at day 0 (g)	1505	1554	
Depletion over 25 d (g)	38	233	
at hatch (g)	1467	1321	Day 25 of incubation
FFM + FM at hatch (g)	1499	1465	Day 25 of incubation