The Significance of Female Body Stores for Egg Laying and Incubation in Dark-Bellied Brent Geese Branta Bernicla Bernicla

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The significance of female body stores for egg laying and incubation in Dark-bellied Brent Geese *Branta bernicla bernicla*

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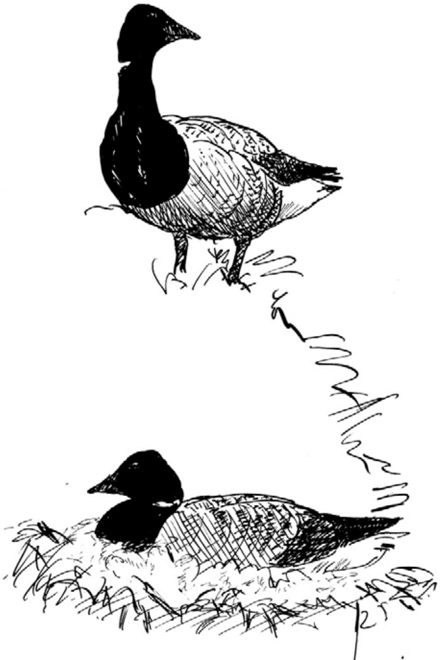

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The probability of successful breeding by Brent geese in the Arctic appears to be positively correlated with the mass of females when they depart from spring staging areas in North-western Europe. To clarify the mechanism behind this relationship we investigated the significance of flown-in female body stores for breeding over six summer seasons (1990–1995) in the Pyasina Delta in Taimyr, Russia. Female Brent Geese were caught upon arrival on the breeding grounds. Changes in female body mass and the timing and duration of nest recesses were recorded via electronic weighing platforms placed under their nests. Average female body masses declined through the breeding season; from 1464 g at arrival to 1269 g after egg laying and 1066 g at hatching, which was supposed to be close to lean body mass. Thus half of the stores were used between arrival and clutch completion, the other half during incubation. All females foraged during incubation. On average they left the nest 13.1 times every 24 hours, resulting in a daily recess time of 198 min during the first 21 days of incubation. Females were less likely to leave the nest during the last three days of incubation. Leaving the nest was risky: 40% of the Brent Goose nests in the study area lost one or more eggs to gulls during absence of the female. We estimated that 52% of the energy required during incubation was derived from body stores and the rest (48%) from food intake.

Key words: *Branta bernicla bernicla*, body stores, incubation energetics, nest-attentiveness, egg predation

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INTRODUCTION

The energetics of avian breeding have been studied in an ecological context in many species. Drent & Daan (1980) introduced the concept of 'capital' and 'income' breeding where capital breeders rely completely on stored reserves for egg formation while income breeders use locally ingested nutrients. Females need energy not only for laying eggs but also during incubation when feeding time is often limited (Meijer & Drent 1999). Moreover, Arctic-breeding birds are very time constrained and have to deal with high costs of migration just before the start of breeding (Klaassen 2003). Brent Geese *Branta bernicla* are an example of such a species: the nominate (dark-bellied) race *B. b. bernicla* migrates about 5000 km from their wintering grounds in NW Europe to their breeding area on the Taimyr peninsula. Ebbinge & Spaans (1995) found that the amount of nutrients individual female Brent Geese stored at the spring staging area in the Wadden Sea (measured as departure weights at the end of May) determined the probability an individual would return to the wintering area with young. This finding indicates that Brent geese are to a certain extent capital breeders.

Some of the body stores Brent Geese accumulate at the spring staging areas will be used as fuel during the migration. To replenish these stores, geese make a stopover in the White Sea and also probably further east during this spring migration (Ebbinge & Spaans 1995, Ebbinge *et al.* 1999). Geese start nesting within a few days of arrival on the breeding grounds in mid-June (Spaans *et al.* 1993, 1998). Food is scarce then, as most of the area is still covered with snow and the vegetation is just starting to grow. It is likely that some of the energy that females need for egg-laying must be derived from stores remaining after migration. Any stores left after egg-laying would be available to be metabolised during incubation. Given the vulnerability of goose nests to avian predators when females are off the nest feeding (Harvey 1971, Inglis 1977, Prop *et al.* 1984, Spaans *et al.* 1993), accumulation of sufficient nutrients before breeding may be crucial to nesting success.

The aim of this study was to determine the extent to which Brent Geese are capital breeders. In other words, how much of the energy females use between arriving on the breeding area and hatching of eggs comes from stored reserves? Therefore we focused on the following questions. (1) What stores do females arrive with at the breeding sites and how much is left after egg-laying? (2) How much do females rely on their remaining stores during incubation? (3) What is the cost in terms of predation risk to eggs of females leaving the nest during incubation? By using weighing platforms under nests we could repeatedly measure changes in body mass without disturbing birds.

STUDY AREA AND METHODS

Dark-bellied Brent Geese were studied in Taimyr, Russia, from 1990 to 1995. The study area is situated in the coastal area north of the Pyasina delta, about 200 km ENE of Dickson, (74°07'N, 86°50'E) (Fig. 1). The coastal mainland and the island Farwaternie consist of low, undulating arctic tundra traversed by a number of small rivers. The vast majority of Brent Geese in the study area breed on the Bird and Beacon Islands (Spaans *et al.* 1998). Big Bird Island (BBI, Fig. 1), is rather flat with mainly tundra vegetation comparable to the mainland. The other Bird Islands are rocky with bare patches, some areas of tundra vegetation, and a more grassy vegetation around colonies of the Taimyr Gull *Larus taimyrensis* (Spaans *et al.* 1993).

We use the same definitions for stores, reserves and lean body mass as Lindström & Piersma (1993). *Stores* are nutrients accumulated in anticipation of certain events, such as long distance migration, egg-laying or incubation. *Reserves* are tissues (protein and fat) that a bird can metabolise in an emergency before it dies of starvation. The *lean body mass* is the (fresh) body mass minus the mass of all extractable fat. Thus, body mass at a given moment is the sum of the mass at starvation, the mass of the reserves and the mass of the stores. In practice it is sometimes difficult to draw the line between stores and reserves.

To determine female body mass at arrival, geese were caught with cannon-nets as soon as possible after arrival (not later than 24 June) at the following locations: the mouth of the Lidia River in 1990 (*n* = 6), along a small river north of Cape East in 1991 (*n* = 2), 1993 (*n* = 3) and 1994 (*n* = 3) and on Big Bird Island in 1995 (*n* = 10) (Fig. 1). Geese were sexed, weighed and marked with coloured leg-rings with alpha-

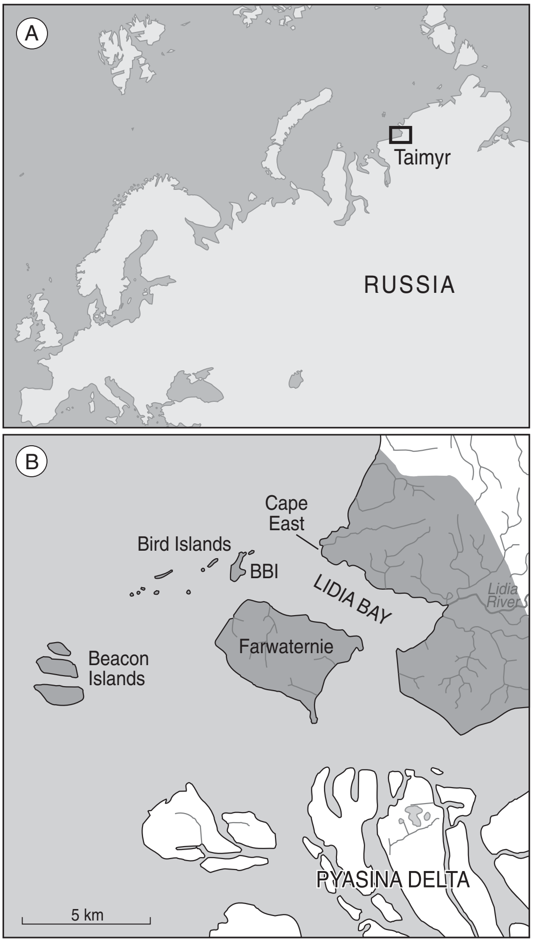

Figure 1. (A) Location of the study area in Taimyr, Russia. (B) The study area, north of the Pyasina-delta in Taimyr, shown by the shaded area. Big Bird Island (BBI) is indicated.

numeric inscriptions. One female, caught on 21 June 1990, had a small brood patch indicating that she had already started egg-laying and is not analysed here.

Because Brent Geese are very sensitive to disturbance during egg-laying, the laying date of the first egg on BBI was not determined directly but calculated from the date of the first observation of a female with goslings by subtracting the length of the incubation period (24 days) and the egg-laying period for an average clutch size (assuming one egg is laid per day).

To record the change in body mass of females during incubation and the timing, number and duration of nest recesses, battery powered electronic weighing platforms were placed beneath Brent Geese nests on BBI in 1991 (n = 5), 1993 (n = 6), 1994 (n = 8) and 1995 (n = 4). The balances were set up as soon as was possible after clutch completion and at least one day of incubation (Fig. 2). Balances were connected to a central computer and were automatically and continuously monitored. Weights were recorded at least once per minute (more frequently if fewer balances were in operation). When the weight changed by 50 g or more it was recorded 10 times in succession and average weight (plus SD) plus nest and time details were stored. The same information was stored after 100 checks without change (or changes less than 50 g). Because the weight on the balance (which included eggs and nest material) varied over time (due to factors such as rainfall), a reliable mass of the female was only obtained when she left the nest. The number of measurements of female body mass per day therefore depended on the number of times she left the nest (referred to as nest recesses). Although the balances were very accurate (± 1 g), variation in measurements occurred due to strong wind or movement of the female. Therefore only (average) masses with a SD <10 g are used for calculation of the body mass. Due to technical problems with the balances and/or the connection with the central computer, registrations were sometimes interrupted. Table 1 provides an overview by year of the nests weighed, detailing the clutch size, period of weighing, number of uninterrupted weighing sequences obtained and success of the nest (which was generally high: 19 of the 23 females hatched their eggs).

In 1992 no data could be collected because the presence of numerous Arctic Foxes *Alopex lagopus* caused the geese to refrain from breeding that year. Foxes did not visit the Bird Islands during the breeding season in the other years (Spaans *et al.* 1998).

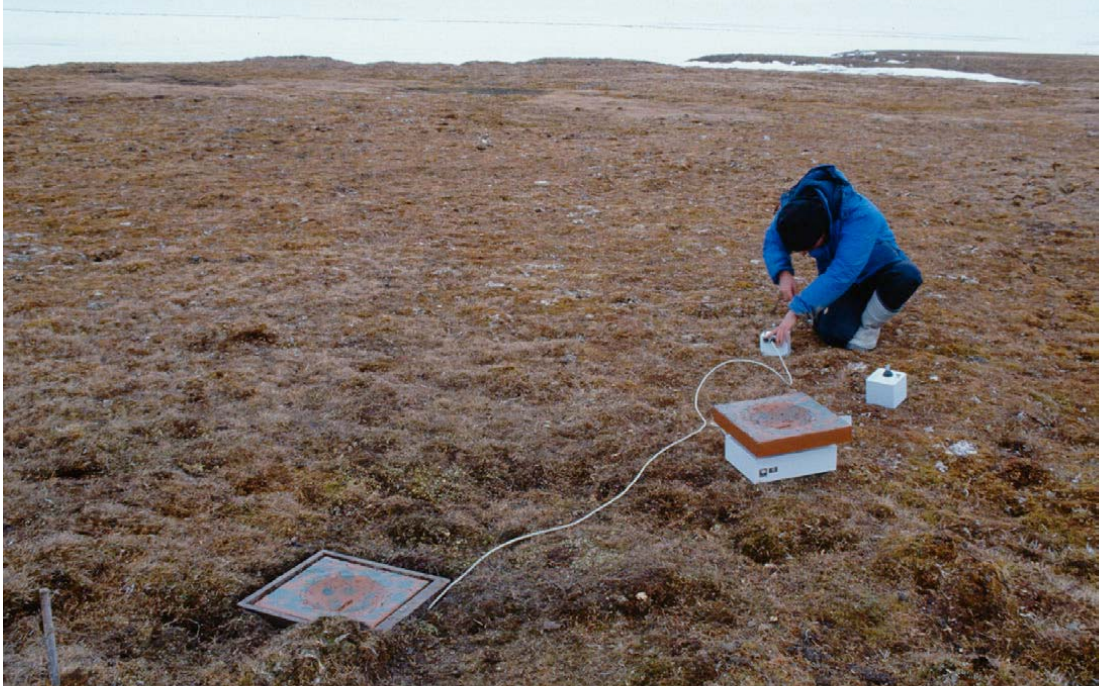

Figure 2. Body mass of Brent Goose females was determined by battery powered balances which were placed beneath nests. One weighing platform has been dug in the ground and is ready for the nest with eggs to be placed on top of it (left foreground). To the right a complete balance is visible. Cables connect each balance with a central computer in a nearby observation hut (photo Jan van de Kam).

From 1990–1995 (except for 1992), the clutch size of a number of Brent Goose nests was checked at least two times during the incubation period to assess possible predation of eggs by avian predators (Gulls *Laridae*, Skuas *Stercorariidae*). These data were used to calculate the probability of a clutch surviving the 24 day incubation period without egg predation, according to the Mayfield method (Mayfield 1975).

The hut on BBI was manned 24 hours per day from the beginning of June until hatching of the eggs in the second half of July. The incubating geese on the weighing platforms could be observed from the hut. Human activity around the hut was restricted to avoid disturbance. The number of geese present on BBI was counted daily from when the first geese arrived until the end of June. All means are listed ± SD.

RESULTS

Female body mass at arrival

Twenty-four adult females were caught upon arrival at the breeding grounds (Table 2) with an average body mass of 1464 ± 110 g. Small sample sizes precluded testing for year effects.

Arrival time and start of egg-laying

All local breeding geese arrived on BBI within 10 to 16 days of the arrival of the first geese (Fig. 3). The first egg was laid 1–4 days after arrival of the first geese in 1991–1994 and 8 days after arrival in 1995 (Fig. 3). Hatching was synchronised; usually all nests on BBI hatched within one week. In 1995, for instance, parents and goslings in 15 of 16 nests left the nest within a 3-day period (20–22 July). Thus it is likely that birds with larger

Table 1. Nests of Brent Geese placed on a weighing platform on BBI. Clutch size was determined on the first day of the weighing period. The period (day/month) is from the day the weighing scale was dug in under the nest until the day the female left the nest. N^{24}: The number of 24 hours periods in which uninterrupted registrations were obtained. Success: the clutch hatched (+), or the eggs were predated or the female left the nest prematurely (-). Overall success rate was 19/23 = 83%.

Year	Nest number	Clutch size	Period	N^{24}	Success
1991	102[a]	3	2/7–20/7	13	+
	101[a]	3	1/7–19/7	10	+
	25	5	8/7–19/7	5	+
	26	2	8/7–15/7	1	+
	15[a]	5	2/7–16/7	3	+
1993	302	2	24/6–7/7	11	-
	303[a]	3	28/6–19/7	17	+
	304[a]	5	28/6–18/7	18	+
	307	3	27/6–19/7	19	-
	312[a]	2	30/6–17/7	15	+
	316[a]	4	30/6–19/7	18	+
1994	401[a]	2	28/6–21/7	11	+
	402	2	1/7–12/7	5	-
	407[a]	5	2/7–21/7	10	+
	409[a]	3	30/6–24/7	12	+
	410	6	7/7–23/7	6	+
	411[a]	6	2/7–21/7	10	+
	416	5	9/7–25/7	9	+
	421[a]	2	5/7–27/7	13	+
1995	501[a]	5	28/6–19/7	22	+
	502	2	29/6–6/7	6	-
	503[a]	5	29/6–21/7	22	+
	504[a]	4	30/6–22/7	21	+

[a] Body mass was recorded at all three stages of incubation.

Table 2. Catch date and body mass of adult female Brent Geese caught at arrival on the breeding grounds.

Year	Date in June	Ring-code	Body mass (g)
1990	15	RPGC	1610
	15	RPGF	1400
	15	RPGH	1380
	16	RPGN	1560
	19	RPGT	1530
	21	RPG1	1330
1991	20	WTRF	1390
	24	O9BT	1460
1993	18	GNGP	1320
	18	GNGT	1420
	20	GNGY	1400
1994	21	GCRC	1510
	21	W9RC	1510
	22	GPG6	1490
1995	13	GPG-	1540
	15	GPG8	1470
	15	GPGT	1620
	15	R5G9	1490
	15	GPG7	1240
	15	GPGD	1550
	17	GAGX	1410
	17	GPG9	1550
	17	GAGD	1280
	17	G=GX	1680
Average (n = 24)		1464 ± 110	
Excluding GPG7,GAGD (n = 22)		1483 ± 95	

clutches had started egg-laying some days earlier than those with a small clutch.

Changes in body mass during incubation

The general pattern of female body mass change during incubation is shown in Fig. 4 for the six females with the best (least interrupted) data in 1993 and 1995. Three distinct periods can be distinguished: Period 1 (days 1–8 of incubation), when female body mass was essentially constant or even increasing slightly; Period 2 (days 8–21), when body mass decreased in a regular and linear fashion; Period 3 (last 3 days of incubation), when body mass decreased rapidly. For 15 females we

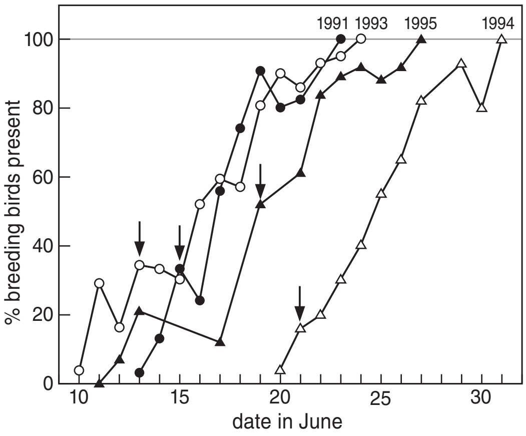

Figure 3. Arrival of breeding birds at BBI in 1991 and 1993–95. The number of Brent Geese present is expressed as a percentage of the total BBI breeding population. Arrows indicate the date of the first egg-laying.

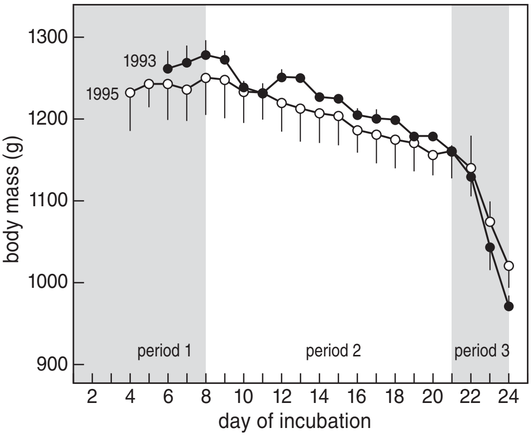

Figure 4. Average body mass during incubation of 3 females (nest numbers 303, 304 and 316) in 1993 and 3 females (501, 503 and 504) in 1995. The three periods during incubation are indicated (see text).

were able to record body mass at the end of all three periods (Table 1). Average body mass for these birds was 1269 ± 67 g (range 1157–1386) at the end of period 1, 1176 ± 70 g (1077–1321) at the end of period 2 and 1066 ± 106 g (951–1304) at the end of period 3, when birds left the nest after hatching. There was no effect of year (ANOVA, $F_{3,11} = 1.18$, $P = 0.36$) or clutch size ($F_{4,10} = 0.84$, $P = 0.53$) on the body mass at the end of period 1.

Female recess time during incubation

All females left the nest daily to feed in the territory around the nest. As far as we could observe, females spent almost all recess time feeding: 90% of the time in 1990 (Spaans *et al.* 1993). Males defended the territory against conspecifics and kept watch over the nest during the absence of the female.

The average daily recess frequency for all balance-females (Table 1) is plotted against the day of incubation in Fig. 5A. During the first 21 days of incubation (period 1 and 2 combined) there was no clear trend and the average recess frequency was 13.1 ± 4 times per 24 h (number of days with 24 h non-stop registration of a female was 197). During period 3 the frequency decreased to 8.4 ± 5.5 times per day ($n = 36$).

Average recess duration showed the same picture as the recess frequency: little variation in the first 21 days and shorter recesses during the last 3 days of incubation (Fig. 5B). The average duration of nest-recess in periods 1 and 2 was 15.1 ± 4.1 min ($n = 197$) and in period 3 was 9.9 ± 6.2 min ($n = 36$).

Average total daily recess time in periods 1 and 2 was 195 ± 70 min day^{-1} ($n = 197$) and during period 3 was 87 ± 75.4 min day^{-1} ($n = 36$) (Fig. 5C). Over the total incubation period females were off the nest on average 178 ± 81 min day^{-1} ($n = 233$). Mean nest attendance was therefore (1440–178)/1440 = 87.6%

Recess time and body mass loss

Average daily body mass loss of the 15 females in period 2 was significantly negatively related to the average daily feeding time; birds feeding for longer lost mass more slowly (Fig. 6). The average recess time per day for these females during period 2 was 208 ± 59 min (range 129–293) and they lost on average 7.0 ± 3.0 g day^{-1} (1.6–10.8) in this period. The intercept for zero recess time,

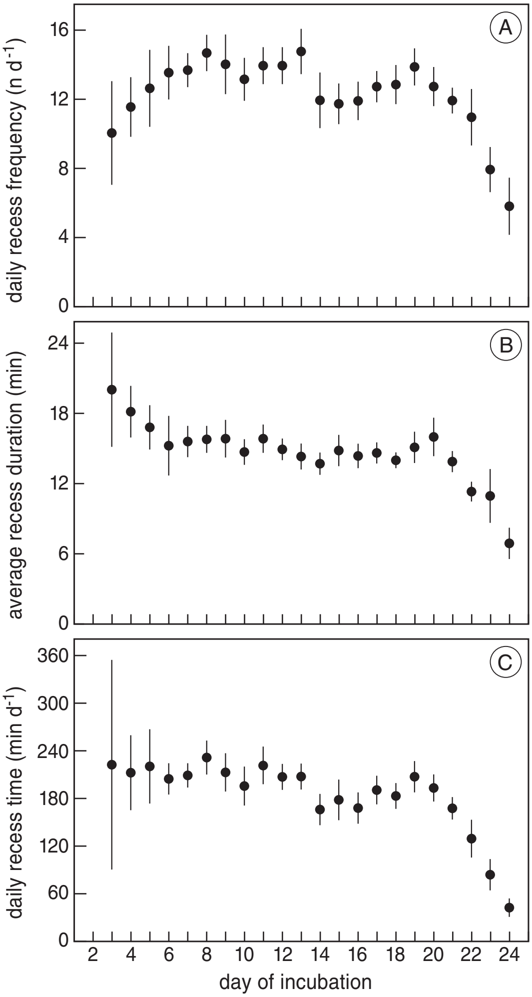

Figure 5. Average daily recess frequency ± SE (A), average recess duration ± SE (B) and average daily recess time ± SE (C) per day of incubation of all females on a balance in all four years.

extrapolating from these data, is 14.4 g body mass loss per day.

Risk of egg predation

Predation of an egg by avian predators occurred only during female recess periods when males strayed too far from the nest giving gulls the opportunity to remove the nests' down cover and take an egg. Such predation of single eggs occurred frequently. The average probability of a nest surviving one day without any egg predation was 0.979 ± 0.0053 (data from all 5 years, totalling 749 nest days from 61 nests, including nests on a balance). The probability of a clutch surviving the full 24-day incubation period without any egg predation was thus $0.979^{24} = 0.60$. This means that on average 40% of the nests suffered from predation of one or more eggs.

Assuming that there is a linear relationship between time off the nest and predation risk, we can make a crude estimate of the predation risk per time unit based on the average daily clutch survival and the average daily recess time during periods 1 and 2. The 195 min. recess time resulted in a clutch survival of 0.979. Thus the survival per hour is $0.979^{60/195} = 0.9935$. The daily recess time (as shown in Fig. 6) can then be converted to daily probability of clutch survival to determine the relationship between body mass loss and predation risk. Plotting the clutch survival over the first 21 days (period 1 and 2) of the incubation (= daily survival to the power of 21) against daily body mass loss shows that the more birds relied on their stores (evidenced by their higher daily mass losses), the higher their clutch survival was (Fig. 7).

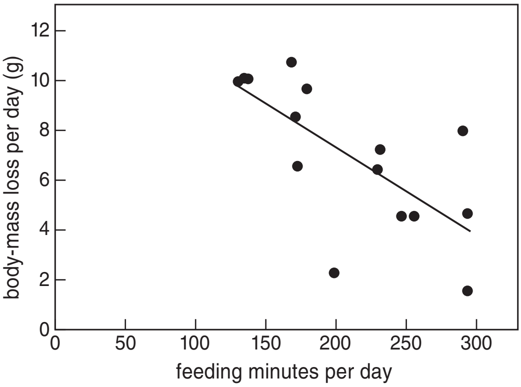

Figure 6. Average daily body mass loss during period 2 as a function of average daily feeding time for 15 females ($y = -0.035x + 14.4$; $F_{1,13} = 12.73$, $R^2 = 0.49$, $P = 0.0034$).

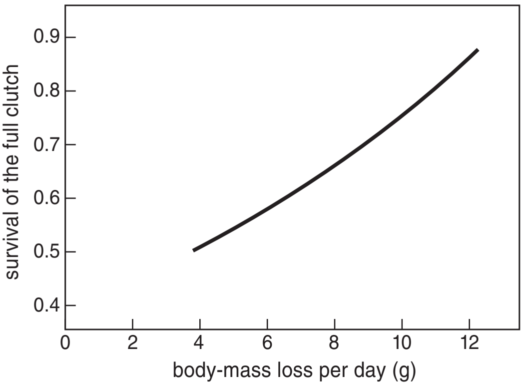

Figure 7. The probability of the full clutch surviving the whole incubation period as a function of female body mass loss per day.

DISCUSSION

Stores at arrival

Carcass analysis of birds collected in winter and spring in NW Europe (Korte 1988) indicates that females have less than 10 g fat left at a body mass of 1025 g, the mass that we treat as representing lean body mass for Taimyr geese. Geese on arrival weighed on average 1464 g (Table 2) and at hatching weighed 1066 g. Because this latter value is the lowest body mass measured during the annual cycle (Ebbinge & Spaans 1995), and very close to the lean mass, we treat 1066 g as representing the average body mass of female Brent Geese without stores. The amount of stores (fat and protein) females had upon arrival can be estimated as 1464–1066 = 398 g. The highest fuelling rate for female Brent Geese, measured on spring staging sites, lies in the order of 15 g day^{-1} (Ebbinge 1989). Therefore it would take 27 days of intensively feeding in the temperate zone (daylight period in spring: about 16 hours) to accumulate such an amount of stores.

Between arrival and clutch completion

The period between arrival and the start of egg-laying was just a few days (Fig. 3). Since most of the tundra was still snow-covered in mid-June and the vegetation just starting to grow, our impression was that it could be hard for the geese to meet their daily demands during this period, let alone to replenish their stores. In Lesser Snow Geese *Caerulescens caerulescens* for instance, the pre-laying period is longer and can be energetically beneficial (Ganter & Cooke 1996). It is known that White-fronted Geese *Anser albifrons* can feed on perennial subterranean plant organs during this period, a highly nutritious food source (Fox & Madsen 1981, Budeau *et al.* 1991). To the best of our knowledge such feeding behaviour has never been observed in Brent Geese (Spilling *et al.* 1994). Thus it seems likely that Brent Geese have to derive most of the energy needed for egg-laying from their flown-in stores.

We measured body mass at arrival but were unable to measure pre-laying mass. However, using clutch-size and body mass of the 15 balance-females we can estimate their pre-laying body mass. The average clutch size was 3.8 ± 1.3 eggs (n = 15) (Table 1) and the average weight of an egg just after clutch completion was 79.5 g (n = 94, Spaans *et al.* 1993), so the total average clutch weight was 3.8 x 79.5 = 302 g. Adding this to the average body mass at the end of period 1 (1269 g), we end up with a minimum expected pre-laying body mass of 1269 + 302 = 1571 g. The average body mass of females caught at arrival (excluding two birds <1300 g that were probably incapable of breeding) was 1483 ± 95 g (n = 22, Table 2). The fact that predicted mass is higher (by 88 g) than measured mass at arrival might mean that body stores contain less water than eggs or that females are able to replenish their stores to some extent between arrival and clutch completion. In Light-bellied Brent Geese *Branta b. hrota* Ankney (1984) found that weight loss as a result of egg laying was also less than the clutch weight (a factor of 0.74). He concluded that at most 71% of the protein in a clutch would be derived from stores (Ankney 1984) and therefore 29% from locally ingested nutrients.

Energy expenditure of incubating females

We have only measured mass but this should be translated into energy. Energetic equivalents of body mass loss during starvation have been obtained for several species of birds (see Table 3). We assume that the measured energetic equivalent of 24 kJ g^{-1} body mass loss found in domestic goose can be applied to incubating Brent Geese. The estimate of the daily energetic cost (without feeding) for our incubating Brent Geese becomes 14.4 g daily mass loss (extrapolated from feeding time = 0, Fig. 6) x 24 kJ g^{-1} = 346 kJ.

The most detailed measurements of the energetic expenditure of incubating waterfowl (without feeding) concern the Common Eider *Somateria mollissima borealis* work done by Gabrielsen *et al.* (1991). They measured the metabolic rate of incubating birds, and found this to be 10% lower than the conventional resting metabolic rate (RMR) determined separately with birds caught on the nest. According to the extensive analysis of Parker & Holm (1990), daily energetic yield from body stores was 490 kJ; this is only 0.75 the RMR measured for birds at this site. RMR has been measured in the Brent Goose in three different studies (collated by Miller & McA. Eadie 2006). For comparison with our estimate from body mass loss in period 2 of incubation we can compute the RMR expected for the mean mass halfway through this period (1223 g). Computation from 6 birds given by Miller & McA. Eadie (2006) (disregarding one outlier) and correcting for body mass by the 0.71 exponent derived by these authors for geese and ducks yields an expected RMR of 452 kJ day^{-1}. The value we estimated for our incubating females was 346 kJ. Apparently our Brent Geese can manage daily energy expenditure at values close to the ‘economising’ Eiders of 0.75 RMR.

Dependence on stores during the incubation period

It seems remarkable that female body mass was stable or even increased during the first week of incubation (Fig. 4). Our impression was that there was no more or better food during this period than later on in the season and the females were not feeding longer than during period 2 (Fig. 5C). Milne (1976) suggested that the fact that the female Eiders he studied became dehydrated during laying and early incubation was caused by the water demands of egg production. The latter could also have been the case in our situation: females recovering in period 1 by replenishing the loss of water associated with egg-laying.

During period 2, from days 8–21 of incubation, body mass decreased linearly (Fig. 4). Daily feeding time of the 15 balance-females during this period was on average 208 min resulting in a limited body mass loss of 7.0 g day^{-1}. Forty-nine percent of the variance in mass loss was explained by the feeding time (Fig. 6). We suspect that quality differences in the food, caused by vegetation differences between the territories (Spaans *et al.* 1993, Spilling *et al.* 1994), can explain another part of the variance in mass loss, as may food quality/quantity differences between years as a result of different weather conditions (Eichholz & Sedinger 1999).

Table 3. Energetic equivalents of body mass loss during starvation

Species	kJ g^{-1}	References
Domestic geese	24	Le Maho *et al.* 1981
Common Eider *Somateria mollissima*	25.9	Gabrielsen *et al.* 1991 Parker & Holm 1990 Korschgen 1977
Great-winged Petrel *Pterodroma macroptera*	22.3	Groscolas *et al.* 1991
Barn Owl *Tyto alba*	23.2–25.4	Handrich *et al.* 1993
White Stork *Ciconia ciconia*	20	Mata *et al.* 2001

The steep decrease in body mass during period 3 can partly be explained by the reduced feeding of the females in this period; many females did not leave the nest at all during the last few days of incubation. However, the average daily body mass loss of 37 g ((1176–1066)/3) is quite large for a fasting bird of this size (Afton & Paulus 1993) and exceeds by far the estimate of the daily mass loss required to balance the cost of incubation in period 2 (Fig. 6). This mass loss suggests that females rely mainly on protein in this period. Although protein yields 18.0 kJ g^{-1} (Pond 1981), the loss of concomitant intracellular water reduces the caloric density of protein tissue to 4–8 kJ g^{-1} (Cherel *et al.* 1988). If a female had no fat left and had to metabolise only protein, the daily body mass loss would be between 346/8 = 43 g and 346/4 = 87 g (assuming the costs are 346 kJ day^{-1}). Given the loss of 37 g day^{-1} that we measured, it is likely that females partly rely on their protein stores in this stage; depletion of most of their available fat could be the main reason for this.

Extrapolation of the regression line in Fig. 6 to feeding time = 0 yields a daily body mass loss of 14.4 g for period 2 of incubation. Since our Brent Geese lost on average 7.0 g daily during period 2, they managed to cover about half of their costs from their stores. To extend these budget estimates to the entire incubation period we assume that period 1 will be comparable to period 2, since the daily recess time (and presumably food intake) is similar (Fig. 5C). Due to the reduced feeding time during period 3, females will depend more heavily on their body stores in these last days of incubation. Taking the reduced feeding time as point of departure, and assuming costs to the female are the same as in period 2, we have computed that only 30% of the costs can be collected by feeding. Overall, we estimate that (21/24 x 0.49) + (3/24 x 0.7) = 52% must be drawn from the body, i.e. the female Brent Goose depends on her body stores for slightly more than one-half of her energy expenditure during the entire incubation period.

Is the intake rate required during nest absence a reasonable figure to balance the budget? For period 2 females were absent from the nest for 208 min each day, and in this time they had to collect at least the equivalent of (14.4–7.0) x 24 = 178 kJ (the act of feeding will add additional costs not estimated here). The rate of collection of at least 178/208 x 60 = 51 kJ metabolizable energy per hour seems feasible: during spring fattening in the Wadden Sea Prop & Deerenberg (1991) found an average hourly metabolizable intake rate of 85 kJ.

Consequences of leaving the nest during incubation

The nest attendance of 87.6% is comparable with values found for other Brent subspecies, which vary from 81.7 to 91.9% and are the lowest of all goose species studied (Afton & Paulus 1993, Eichholz & Sedinger 1999). Females leaving the nest risk losing eggs to predators, and the probability of egg loss in our study increased with the time spent feeding (Figs 6 and 7). Overall, 40% of the nests we studied suffered egg predation.

If there is little food, however, there is little point in attempting to feed. In contrast to our results, Madsen *et al.* (1989) and Spaans *et al.* (1993) found that Brent Geese spent an increasing amount of time off the nest as the incubation period progressed. This may have been caused not only by the birds' declining stores but also by an absence or scarcity of food early in incubation. In general, the availability of food will improve over time as snowmelt progresses and plant production increases. Consequently, Brent Geese breeding in colder conditions (in cold years or at higher latitudes) will depend even more on their body stores, particularly during the first part of incubation (Eichholz & Sedinger 1999).

Females arriving in the breeding area in very good condition (Table 2) face a trade-off between laying a larger clutch or saving stores to reduce feeding during incubation. Our balance-females with large clutches (5 or 6 eggs, Table 1) started incubation with comparable stores to the females with smaller clutches (1271 vs. 1266 g respectively). It seems that females choose the larger clutch option rather than saving stores to reduce feeding. From the predation point of view this is understandable. An investment in an extra egg roughly means 3 g stores per day less available to metabolise. This increased the predation risk by about 10% (Fig. 7). In other words the probability that this egg would survive the incubation period, despite the extra recess time, was about 90%.

This study shows the 'position' of Dark-bellied Brent Geese on the continuous scale between the extremes of 'capital' and 'income' breeders (Klaassen 2003). During incubation geese draw heavily upon stores that remain after migration, and the more a bird has to forage away from the nest the greater the risk of nest predation. The body condition at departure from spring staging areas 5000 km away is therefore an important determinant of the breeding success of Taimyr Brent Geese. Birds must retain sufficient stores to produce a clutch, and after that the remaining stores cover about half the costs during incubation. Females arriving too light can only lay a small clutch and will have to spend a more time feeding during incubation, with an increased predation risk to the clutch.

The geese we studied are those that arrived in the breeding area in June; these could well be only those birds that have sufficient stores to start breeding. Later in the season thousands of non-breeding (adult) Brent Geese show up in our area, potentially being late or light birds that did not attempt to breed. The average goose in our sample may not necessarily be the average goose in the greater population.

Due to the short summer season at the high latitudes of Taimyr Peninsula (our study site was at 74°N) nesting must start as soon as possible after arrival. The long flight with limited refuelling possibilities between Europe and Taimyr will be one reason why Brent Geese cannot arrive with sufficient stores to incubate without leaving the nest. White-fronted Geese, in contrast, breed in the same area in Taimyr but manage to incubate continuously (Spaans *et al.* 1999), as their final spring fattening areas in central Russia are much closer (Mooij *et al.* 1999). Moreover their costs during incubation are comparatively lower due to the larger size of this species (Miller & McA. Eadie 2006).

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SAMENVATTING

In het Noord-Siberische broedgebied van de Zwartbuikrotgans *Branta bernicla bernicla* is onderzocht in hoeverre de vrouwtjes tijdens de voortplantingsperiode afhankelijk zijn van de 'ingevlogen' reserves. De hoeveelheid meegebrachte reserves werd geschat door zo snel mogelijk na aankomst in het broedgebied rotganzen te vangen en te wegen. Gemiddeld wogen de vrouwtjes 1464 g bij aankomst. In vier jaren werden weegschalen onder rotgansnesten ingegraven. Via een computer werden gewichtsverloop en verblijfstijd op het nest automatisch geregistreerd. Het gemiddelde gewicht aan het begin van het broeden was 1269 g, bij het uitkomen van de eieren 1066 g. Aangenomen wordt dat bij 1066 g de reserves vrijwel geheel opgebruikt zijn. De helft van de ingevlogen reserves werd besteed in de tijd tussen aankomst en het begin van het broeden aan het leggen van de eieren. De andere helft diende als energiebron tijdens het broeden. Dit bleek echter onvoldoende om non-stop te broeden, zoals een aantal grotere ganzen doen. Alle vrouwtjes verlieten daarom geregeld het nest om bij te eten. Gedurende de eerste 21 dagen van de broedperiode verlieten ze gemiddeld 13,1 keer (in totaal 198 minuten) per etmaal het nest. Tijdens de eetpauzes bestaat het risico dat er een of meer eieren uit het nest gestolen worden door meeuwen. Dit gebeurde in 40% van de rotgansnesten. De kans dat het gehele legsel de broedtijd overleefde, werd voor de vrouwtjes die relatief vaak van het nest gingen (en dus minder op hun reserves teerden), geschat op 50% en voor de vrouwtjes die weinig van het nest gingen (meer op hun reserves teerden) op 90%. Tijdens de laatste drie dagen van het broeden gingen de ganzen minder vaak van het nest dan ervoor of zelfs helemaal niet meer. Met behulp van een aantal aannames over de kosten van het broeden en de energetische waarde van de reserves werd geschat dat de voedselopname tijdens de eetpauzes minimaal 51 kJ per uur zou moeten zijn. Dit is wat lager dan de opnamesnelheid tijdens het opvetten in het waddengebied. Uitgedrukt in energie werd geschat dat ongeveer 52% van de energiebehoefte tijdens het broeden afkomstig was van de reserves en de rest bijgegeten moest worden.

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