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Energy limitations for spring migration and breeding: the case of brent geese *Branta bernicla* tracked by satellite telemetry to Svalbard and Greenland

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Clausen, P., Green, M. and Alerstam, T. 2003. Energy limitations for spring migration and breeding: the case of brent geese *Branta bernicla* tracked by satellite telemetry to Svalbard and Greenland. – *Oikos* 103: 426–445.

Brent geese were tracked by satellite telemetry from spring staging areas in Denmark to Arctic breeding areas in Svalbard and Greenland in 1997 and 2001. From estimated departure masses and carcass analysis we used flight mechanical theory to estimate maximum flight ranges of both sexes, and remaining stores of fat and protein upon arrival in females. Model predictions suggested that all birds but one exceptionally thin male could easily reach Svalbard, but that approximately one third of the males and half of the females would have problems with flying to Greenland. Nevertheless, some birds even flew longer than the models predicted. In addition, females predicted to be capable of making the flight to Greenland, were predicted to arrive almost lean of fat. This contradicts our expectation that these birds are capital breeders – that they depend on endogenous stores of fat and protein when initiating and incubating their eggs. We discuss how the Greenland breeding sub-population during 1985–1998 has been able to grow at the same rate as the sub-population breeding in Svalbard, despite the added flight distance of 700–1000 km, and despite the birds predicted shortage of fat stores on arrival. We suggest four hypotheses that alone or in combination could explain the discrepancy between model predictions and observations. These are that most birds: (1) refuel on stop-overs in Spitsbergen en route to Greenland; (2) pick favourable tail-winds enabling them to reduce flight costs; (3) fly in formation and thereby save energy; and/or (4) undergo gut atrophy immediately prior to departure, and use the nutrients mobilised by catabolism of the digestive system to build larger pectoral muscles. The latter option would both reduce their airframe fraction, and increase their fat and flight-muscle fractions, enabling them to fly longer. We conclude that the latter option seems less likely to operate in brent geese.

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Arctic breeding geese usually arrive to their breeding areas when these are frozen, almost totally covered by snow, and with poorly developed if any vegetation (Madsen et al. 1989, Prop and de Vries 1993). Access to supplementary feeding upon arrival is therefore restricted, and Arctic geese are generally thought to rely on endogenous body-stores of fat and protein for laying their eggs (Ankney and MacInnes 1978, Raveling 1979, Ankney 1984) – they are so-called 'capital breeders'

(Drent and Daan 1980, Meijer and Drent 1999). When temperatures are too low or snow conditions too adverse laying is delayed and clutch sizes are reduced (Barry 1962, Ganter and Boyd 2000). In exceptionally cold years brent geese may even refrain from laying eggs at all (O'Briain et al. 1998). Females that incubate their clutch without leaving the nest appear to be more successful than females who frequently make recesses to feed – especially because the latter suffer more from

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predation than the former (Harvey 1971, Inglis 1977, Raveling and Lumsden 1977, Prop et al. 1984, Thompson and Raveling 1987, Madsen et al. 1989). To improve the chances of successful breeding, the geese would benefit from arriving with as large body-stores of fat and protein as possible, but meeting this goal is constrained by limited fuel-carrying capacity of birds (Hedenström and Alerstam 1992).

A satellite telemetry study of brent geese in spring 1997 demonstrated that a pair of light-bellied brent geese *Branta bernicla hrota* (Müller) made a 3300 km flight from a spring staging area in Denmark to northern Greenland without refuelling (Clausen and Bustnes 1998). According to model predictions from flight mechanical theory (Pennycuick 1975, 1989) the flight performed by the female was longer than the theoretical maximum flight range possible for a goose with her body mass and wing characteristics, and therefore no body-stores would remain at arrival that could be invested in breeding. The actual pair followed by telemetry indeed also returned without goslings (Clausen and Bustnes 1998). The tracked pair of brent geese belonged to a colony at Kilen in northern Greenland. The Kilen population constitutes ca 20% of the total flyway-population of East Atlantic light-bellied brent geese, which includes a few pairs breeding in adjacent parts of northern Greenland (Hjort 1995), many more in the Svalbard archipelago (ca 80% of the total), and very few pairs in Frans Josefs Land (Clausen et al. 1999). The Kilen brent goose colony was discovered in 1985 and that year numbered 850 birds, and successful breeders had an estimated average brood size of 3.44 goslings/pair (Hjort et al. 1987). This brood size exceeds corresponding figures from Svalbard (three study years, with range of 2.36–3.0, Clausen et al. 1999). In the summer of 1998 Kilen was revisited and now held 1100 adults/yearlings, but only 37 (between 25 and 49) goslings were present due to heavy fox predation (Clausen and Laubek 1999). The Kilen segment of the flyway-population in the 13-yr period from 1985 to 1998 thus increased from 850 to 1137 birds, while the non-Kilen segment increased from 3750 to 4963 birds (estimated as total flyway-population excluding Kilen birds; total autumn population estimates of 4600 birds in 1985/86 and 6100 birds in 1998/99; Clausen et al. 1998 and unpubl.). These coarse data suggest annual growth rates of 2.26% and 2.18% for the two sub-populations, respectively.

In this paper we combine data from a new satellite telemetry study carried out during spring migration 2001 with a reanalysis of the data from the 1997 tracking study. We compare overall flight distances covered by the satellite tracked birds with predictions of maximum flight ranges derived from flight mechanical theory (Pennycuick 1975, 1989 – as updated by Pennycuick 2002). Furthermore we use this theory in combination with data on body composition of our birds to

predict remaining fuel stores on arrival at the breeding grounds. We aim to explore to which extent brent geese migrating to Svalbard and Greenland from spring staging areas in Denmark carry along stores of fat and protein for breeding.

Methods

Capture sites and colour-ringing

We caught light-bellied brent geese by cannon-netting on two occasions: 17 birds on 15 May 1997 at Agerø, Denmark (56°43' N 8°33' E) and 31 birds on 16 May 2001 at Mågerødde, Denmark (56°47' N 8°33' E). Both sites are major spring staging sites within the Agerø area, recognised as the most important spring staging area of the population since the mid 1980s (Clausen et al. 1998). We ringed all birds with individually recognisable engraved colour-rings that can be read at distances up to 300–400 metres under good conditions (Clausen and Percival 1992).

Body mass at capture and estimated mass changes between catch and departure

Body mass at capture was measured with a 0–2.5 kg Pesola spring balance (estimated accuracy 0.01 kg) and we define this measure as m_{capture} .

During the spring period brent geese rapidly build up body-stores, and most birds typically add 0.3–0.5 kg during April and May (Ebbinge 1989, Ebbinge and Spaans 1995). To incorporate a measure of body mass gained in the period between catch and departure (see below), we regularly assessed abdominal profile indices (API, Owen 1981) of individually recognisable birds, and of the population generally by sampling flocks of unringed birds, in the second half of May. API's are known to reflect body mass changes in swans (Bowler 1992) and geese (Drent et al. 2003), and we used a scoring system specifically developed for brent geese (indicated in Fig. 1). The identified API changes were subsequently recalculated to an estimate of body mass change, assuming that a change in API of 1.0 is equivalent to a body mass change of 0.16 kg for both females and males (R.H. Drent and co-workers, unpubl.), and call this estimate m_{change} .

From the measured body mass and the increment after capture we estimated the departure body mass as:

$$m_{\text{departure}} = m_{\text{capture}} + m_{\text{change}}$$

Body composition of brent geese

In order to compute maximum flight ranges with methods outlined below, it is essential to know the fractions

of the birds total body mass at departure that consist of fat and flight-muscle, respectively. We therefore compiled published and unpublished information on body composition of light-bellied brent geese. We base our analysis on samples from pre-migratory and pre-breeding 'Atlantic brant' – a flyway-population of brent geese of the same sub-species as those we work with. They have different geographic origin (Reed et al. 1998a), but perform spring and autumn migratory flights of 2800–3800 km (Vangilder et al. 1986), i.e. flights comparable to those made by the brent geese we studied. The regression analyses of fat contents of brent geese are based on carcass analysis of: i) pre-laying and breeding birds sampled on Southampton Island, mid June to early July 1979 and 1980 (excluding moulting birds, which undergoes flight muscle atrophy, Ankney 1984); ii) pre-migratory birds sampled in James Bay, late May and early June 1990 and 1991 (A. Reed and G. Gauthier, unpubl.); and iii) pre-migratory birds sampled on Long Island, New York, early May 1984 (Vangilder et al. 1986). The carcass analysis of the James Bay birds was made according to methods given in Gauthier et al. (1992, G. Gauthier pers. comm.), and we consider the three studies as being directly comparable. The analyses of flight muscle masses are based on data from Southampton Island and James Bay only (Vangilder et al. 1986 did not consider flight muscle mass). Data available to us were means, standard errors of the mean (se) and sample sizes (n) of body mass (wet mass, excluding gut contents), total fat mass (dry mass), and flight-muscle mass (dry mass).

From these data we developed regression models describing the body composition of brent geese of both sexes in relation to their body mass. The three studies of body composition were based on highly different numbers of birds. In order to give all the samples similar weights in the regression analysis, we calculated standard deviations ($sd = se \times \sqrt{n}$), assumed normality, and used the mean and sd to generate 500 random estimates of total fat and flight-muscle mass for each body mass category. The linear regression models were subsequently based on the random generates. The derived regression lines were used to estimate fat (dry mass) and flight-muscle mass (dry mass) of departing brent geese. The values needed for flight range computations below are based on wet mass. We assumed that the ratio between dry and wet fat mass was 1:1, and multiplied the dry flight-muscle mass by 4 to estimate wet flight-muscle mass (Ankney 1984 measured a ratio between dry- and wet flight-muscle mass of 1:4). The needed fractions are then computed by first estimating the fat and muscle masses for a given departure mass, $m_{\text{departure}}$, from the regression formulae – secondly dividing the estimated value with that departure mass.

Predicting maximum flight ranges and remaining body stores upon arrival

We used the estimated departure body masses, fat and flight-muscle fractions, in combination with data on wing-span and wing-area collected from one male and one female (Table 1), to predict maximum flight ranges of both sexes, and remaining body stores of fat and protein of females arriving to Svalbard and Greenland, respectively. Predictions were made with the most recent version of the software package 'Flight for Windows' (ver. 1.11; Pennycuik 2002) which computes flight performance of birds based on a mechanical flight theory (Pennycuik 1975, 1989). This new software allow use of protein in addition to fat as fuel for flight (Pennycuik 1998), and several parameters are recomputed at 6 min intervals, using a 'time-marching' approach (sensu Pennycuik 1998). These include the birds' body mass, m ; the energy density of fuel, e , (allowed to change during the flight, dependent on which combination of fuel is burned – fat and/or protein); the chemical power estimate, P_{chem} (being mass dependent); and the effective lift:drag ratio, N , of the modelled birds (being defined both from the birds body mass and the chemical power, as: $N = mgV / (\eta P_{\text{chem}})$, where η is the conversion efficiency, g is the acceleration due to gravity, and V is the birds airspeed) (see Pennycuik 1998, Pennycuik and Battley 2003 for details). This new software also incorporates new default values that are different from those used by Pennycuik (1989). These changes are based on new knowledge about essential parameters, such as profile power ratio (Pennycuik 1995), body drag coefficient (Pennycuik et al. 1996a), and the ratio between minimum power speed and actual flight speeds (Pennycuik 2001).

We generally used default parameters and computation decisions of the software as listed in Table 1. Whenever deviations from default values were applied, as indicated and explained in Table 1, the decision to do so was based on comparisons between test model outputs and actually observed flight behaviours of heavy-fuelled dark-bellied brent geese observed on spring migration above Lund in southernmost Sweden (Green and Alerstam 2000).

Satellite transmitter deployment and programming

In 1997 we equipped five birds with a 22 g Microwave Telemetry Inc. PTTs (platform transmitter terminals) (standard 20 g PTTs supplied with a stronger antenna). In 2001 we used standard 30 g Microwave PTTs on eight birds. In order to avoid potential negative influence of radio transmitter attachments on the breeding performance of females (Ward and Flint 1995), the intention was to track males only. However, in 1997 we

Table 1. List of values and criteria used to compute maximum flight ranges and body composition changes of migrating light-bellied brent geese with Flight for Windows v. 1.11 software (Pennycuick 2002). Further details see Pennycuick (1989, 1998). Values and criteria given in bold deviates from default.

Symbol	Variable	Value used
b	Wing-span (m)	1.125 (female) 1.21 (male)
S	Wing-area (m ²)	0.142 (female) 0.165 (male)
r	Aspect ratio	8.89 (female) 8.87 (male)
C _{Db}	Body drag coefficient	0.1
e _{fat}	Fat energy density (J kg ⁻¹)	3.90 × 10 ⁷
e _{prot}	Dry protein energy density (J kg ⁻¹)	1.83 × 10 ⁷
g	Gravity (m sec ⁻²)	9.81
h _{prot}	Protein hydration ratio	2.2
k	Induced power factor	1.2
k _{mit}	Mitochondria inverse power density (m ³ W ⁻¹)	1.20 × 10 ⁻⁶
r _{cr}	Circulation and respiration factor	1.1
r _v	Ratio V:V _{mp}	1.25^s
t _{calc}	Calculation interval (min)	6
η	Conversion efficiency	0.23
ρ	Air density (kg m ⁻³)	1.23 ^s
Criteria		
	Minimum energy from protein (%)	5
	Protein burn criterion	Constant specific work
	Mitochondria control	Constant mitochondrial power density
	Flight style	Continuous flapping
	Air speed control	Constant ratio V:V_{mp}[#]

We measured the wing-span and wing-area (including the back) on two adult birds, a male and a female, found dead in Denmark, winter 2000/01 (method after Pennycuick (1999)). ^sThe default value is 1.20. We used a value of 1.25, because the default predicts lower airspeeds than the average of 19.0 m/sec observed at Lund in spring for a bird with the average body mass size and wing morphometrics given by Green and Alerstam (2000). ^sAssume the birds fly at sea-level, supported from estimated flight heights of 4,512 light-bellied brent geese, 75% of which flew less than 10 m above sea-surface (M. Green et al. unpubl.). [#] We used the option with constant ratio V:V_{mp}, because this has the implication that birds will initiate their flight at higher speed and gradually lower the speed as flight progresses and they loose body mass, as observed in dark-bellied brent geese (Green and Alerstam 2000).

encountered problems with proper sexing, and selected individuals among the largest birds. Subsequently we found by behavioural observations of the birds in the field that three of the birds were adult males and one an adult female (paired to one of the males with a PTT). In 2001 we had no problems with sexing and applied PTTs to adult males only. Body masses of equipped birds ranged from 1.66–1.99 kg, i.e. PTTs weighed less than 2% of the birds body mass at capture. We attached the PTTs to the backs of the birds just behind their shoulders with Loctite Superattak glue. In addition we fastened the transmitters to the birds with knickers elastic harnesses (2 g) following guidelines given by Glahder et al. (1998).

In 1997 the PTTs were programmed to transmit according to the following protocol during spring migration: 8 hours on–15 hours off, 15 May–15 June. In 2001, due to improved battery quality, we let the transmitters operate continuously in 699 hours, i.e. from 16 May–14 June 2001.

In 1997 we successfully tracked four birds with satellite telemetry to potential breeding sites in the Arctic (cf. Clausen and Bustnes 1998 for details) – in 2001 we followed seven birds (this study). Each PTT was recognised by a 5-digit individual ID code – throughout this paper we use single letters as identification codes for

individual birds: A, B, C, D (1997 birds) and E, F, G, H, I, J, K (2001 birds).

Evaluation of flight paths, distances and stop-over sites

Signals transmitted by the PTTs were recorded by the ARGOS satellite system (Fuller et al. 1995, Beekman et al. 1996). Each position provided by ARGOS is stamped with date and coordinated universal time (UTC), and a measure of position accuracy, given in six location classes. Four of these are based on at least four received PTT messages: 3 (accuracy < 150 m), 2 (150–349 m), 1 (350–1000 m), 0 (> 1000 m), the remaining two, A and B, are based on three and two received messages, respectively, with no estimate of location accuracy (ARGOS 1996). Recent studies (Hays et al. 2001, Vincent et al. 2002) suggest that the accuracy of class A positions may be as good as class 1 positions and better than class 0 positions. The accuracy of class B positions may be better (Hays et al. 2001) or worse (Clausen and Bustnes 1998, Green et al. 2002, Vincent et al. 2002) than class 0 positions. Because of the uncertainty of the accuracy of the B location class, we only used these after careful inspection (see below).

Generally, the 1997 22 g PTTs gave fewer and less accurate positions than the 30 g PTTs used in 2001. This difference was partly because the PTTs transmitted continuously in 2001 and only eight out of 23 hours in 1997, but the number and accuracy of received positions was also dependent on satellite orbits (one additional satellite active in 2001), bird behaviour, local conditions and within-year differences in transmitter quality. In 1997 we received between 0 and 10 positions per day and bird during the study period, generally more in periods with long-distance migratory flights (2 to 17 per day and bird or pair, birds C and D combined). In 2001 we received between 0 and 60 positions per day and bird during the study period, and between 8 and 47 per day and bird on days with migratory flights.

We carefully analysed all received positions, and rejected those that were inconsistent with the distance from one position to another and led to unrealistically high flight speeds. In 1997 we had to evaluate all positions received, but only accepted low-quality positions (0, A and B) when flight speeds between adjacent positions in time and space were less than 90 km/h (Clausen and Bustnes 1998); in 2001 we were fortunate to receive a surplus of positions, and therefore only used class 3, 2, 1, 0 and A positions, rejecting all class B positions, and still rejecting class 0 and A positions which led to ground speeds (resulting speed over the ground incorporating local wind effects, M. Green, unpubl.) above 120 km/h. If more than one position were available within the same hour, we selected the position with highest quality (if class 3, 2 or 1 positions were available), else we selected the class 0 or A position which gave the best spacing in time between adjacent positions.

The location times in UTC were used for all calculations of time intervals between positions. We calculated two estimates of total travel distance between the spring staging area in Denmark and the final summer destination. The first and 'shortest' estimate is based on locations of high quality only (ARGOS classes 1,2,3), and assumes that the birds fly between these locations along orthodromes (great circles, Imboden and Imboden 1972). The 'shortest' total travel distance is thus the sum of calculated orthodromes between Denmark and the summer destination. The second and 'longest' estimate is based on the selected locations according to criteria outlined above (including ARGOS classes 0 and A, in 1997 also B), and assumes that the birds fly between these locations along loxodromes (rhumb lines, Imboden and Imboden 1972). The 'longest' total travel distance is thus the sum of calculated loxodromes between Denmark and the summer destination. Estimates of detours were made by comparing the total travel distances with that of the shortest possible route – an orthodrome directly from the departure site in Denmark to the arrival destination in the Arctic.

In our analysis of stopover areas we have generally only used high-quality positions (3, 2, and 1 if available) to locate them, while lower quality positions were used to analyse departure and arrival times from these areas. Stops were defined as periods with flight speeds of less than 20 km/hour (6 m/sec), lasting at least 1 h. Stops exceeding 48 hours were classified as long-time stopovers and those lasting less than 48 hours as short-time stops (Green et al. 2002). The basis for this division is that we find it more likely that stops exceeding 48 hours are real foraging stopovers with the possibility of net energy gain for the birds. We evaluated the potential feeding opportunities on stopover sites by consulting detailed maps of Norway and Svalbard published by Statens Kartverk, Norway.

Timing of migration

To assess whether the brent geese followed by satellite telemetry 'behaved naturally' – at least when initiating their spring migration, we compared departure dates of the transmitter birds with departures of birds in the population as a whole. Departures of the latter were based on a compilation of counts of staging brent geese in the Agerø area in the last week of May, in combination with spring migration counts of light-bellied brent geese from Lista Bird Observatory, southwestern Norway (58°07'N 6°34'E). Here observers make daily observations of bird migration from early May until early June, usually from 1 hour before sunrise to noon, frequently extending the observation period on days with mass migration. Most years between 1000 and 3500 light-bellied brent geese are observed on spring migration when passing this island (M. Green et al. unpubl.), corresponding to ca 15–60% of the total population.

Subsequent breeding success

Brent goose families migrate together to the wintering areas, and families are generally associated even in spring (Reed 1993). To assess whether the brent geese followed by satellite telemetry returned with goslings, we searched for ringed birds when they returned to their wintering areas. Birds were searched for during autumn and winter 1997/98 and 2001/2002 at Lindisfarne, England, one of the most important wintering areas of the population (Clausen et al. 1998); and in Denmark when returning in springs 1998 and 2002. The breeding success of the population as a whole was also determined by coordinated counts of adults and juveniles in Lindisfarne and Denmark during November and December 1997 and 2001 (methods follows Clausen et al. 1998).

Results

Captured birds

In this paper we are mainly concerned with the migratory performance of adult birds, i.e. potential breeders, of known sex. Six of the 17 birds caught in 1997 and five of the 31 birds caught in 2001 were juveniles, and four of the adults caught in 1997 have not subsequently been sexed based on behavioural observations in the field. This leaves seven adult birds from 1997 (three females and four males) and 26 adult birds from 2001 (12 females and 14 males) for in-depth analysis.

Among these, the birds subsequently followed by satellite telemetry (10 males and one female, Appendix 1 and 2) and their mates are of major interest. It is generally thought that paired birds migrate together, and this is verified by tracking light-bellied brent geese from Iceland across Greenland (Gudmundsson et al. 1995), and from Denmark to Greenland (birds C and D, Clausen and Bustnes 1998). In addition to the paired birds with satellite transmitters, we know from field-observations that bird A from 1997 and birds F, H, I, and K from 2001 were accompanied with females we also had caught (Appendix 2).

Departures

In 1997 mass departure of brent geese occurred at Agerø in the morning of 30 May, when the staging number of brent geese declined from 2869 on 29 May to 530 on 30 May. In agreement with these observations northbound mass migration of 2469 birds was observed at Lista on 30 May, the only date with > 200 birds migrating that year. The number migrating is higher than the decline observed at Agerø, showing that birds also departed from other spring staging areas in Denmark this day. Three of the birds with satellite transmitters also departed on 30 May, while the fourth bird probably departed on 29 May (Appendix 2).

In 2001 birds departed in two waves – the first with 3344 birds migrating north at Lista mostly in the afternoon/evening of 25 May (none observed between 5:30 am and 10:50 am) and the morning of 26 May (none observed between 11:33 am and 7:00 pm), and the second with 1140 birds migrating in the morning of 31 May (none was seen on 30 May, despite 13½ hours observation). Five of the birds with satellite transmitters departed in the first wave on 25–26 May, the remaining two with the second wave in the evening of 30 May (Appendix 2). The second departure was also noticed in the staging areas, with 1300 birds staging at Agerø and Mågerødde on 30 May, and 8 flocks totalling 636 birds departing in the evening, leaving 664 birds at the communal night roost. Next morning on 31 May only 280 birds remained in the area.

Capture mass, condition changes and estimated departure body mass

Body mass of captured males averaged 1.80 kg and that of females 1.72 kg (Appendix 1).

In the 1½–2 weeks after capture and prior to departure, the API's of the brent geese increased significantly in both years, but apparently at a lower rate during 2001, when the birds had attained a higher abdominal profile score in mid-May when we caught birds (Fig. 1). We used regression analysis to estimate the increase in API from catch date to mass departure dates. In 1997 API scores increased from 2.42 on 15 May to 2.93 on 30 May 1997. This increase in API score represents a body mass gain of 81.75 g (5.45 g/day). In 2001 API scores increased from 3.01 on 16 May to 3.23 on 25 May and 3.34 on 30 May. These increments in API scores represent body mass gains of 36.2 g and 53.0 g (3.78 g/day) for birds departing with the first and second mass departure wave, respectively.

Assuming that all captured birds had experienced similar mass gains, with the year-specific difference outlined above, we estimated their body mass at departure. For birds with unknown departure date (i.e. birds not associated with satellite transmitter birds) we assumed departure on 25 May 1997 (when most birds departed) and 30 May 2001 (departing with the second mass departure wave). Resulting estimated departure body masses of males averaged 1.86 kg (range 1.45–2.13 kg) and that of females 1.78 kg (range 1.53–1.89 kg, Appendix 1).

Body composition of brent geese

The regression analysis showed that the fat mass and flight-muscle mass of birds increased significantly with total mass (Fig. 2). For both sexes, the prominent fat accumulation had the impact that the fat fraction increases considerably whereas the flight-muscle fraction declines slowly with a positive change in body mass (Fig. 2).

Migratory routes, flight distances, stopovers and detours

In 1997, two birds migrated to summer destinations in Svalbard (Clausen and Bustnes 1998, Fig. 3). Bird A migrated to Murchisonfjorden in Nordaustlandet where it spent the summer. Bird B was located at Woodfjorden in northern Spitsbergen, a known moulting site of light-bellied brent geese (Mehlum 1998), when we lost contact. The two other birds – the paired birds C and D, migrated to Peary Land in northern Greenland, and made the flight from Denmark to Greenland without stopping at any sites where they could have been feed-

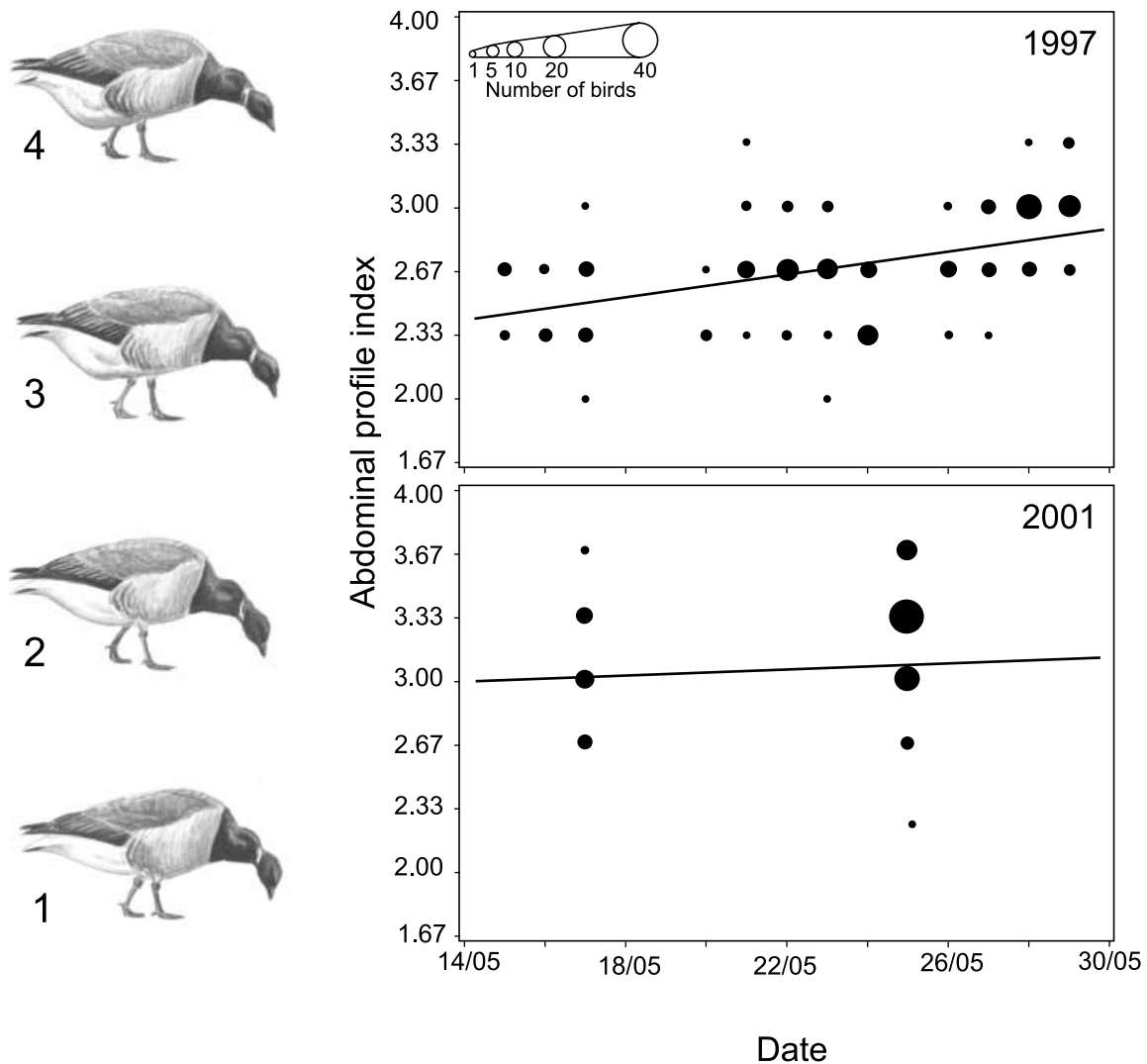


Fig. 1. Development in abdominal profile indices (APIs) of light-bellied brent geese during the second part of May at Agerø 1997 and Mågerodde 2001, respectively. Birds are scored in 10 categories, ranging from 1 to 4 – the drawings indicate the four integer categories. Birds between 1 and 2, but closest to 1 is scored as 1.33, those closest to 2 as 1.67, likewise for birds between 2 and 3, and between 3 and 4. The size of circles in the diagrams gives the number of individually recognisable birds classified to each profile index per day. Lines are simple linear regression models, fitted to the data (counting days from 15 May = 1). 1997: $API = 2.38 + 0.0340 \times \text{day}$; $r^2 = 0.29$, $P < 0.0001$. 2001: $API = 3.00 + 0.0078 \times \text{day}$; $r^2 = 0.06$, $P < 0.0085$.

ing (Clausen and Bustnes 1998, Fig. 3). In 2001, all seven birds initially migrated to stopover sites on western Spitsbergen. Six of them continued to summer destinations in the northern (birds F and G), eastern (bird H) or central parts of Spitsbergen (birds E, J and K, Fig. 3). The remaining bird (bird I) continued to Kilen in northern Greenland, where it spent the summer (Fig. 3).

All birds made only short-time stopovers between Denmark and their first destination in the Arctic (Fig. 3). None of these were made in terrestrial or shallow-water habitats, where they potentially could have been feeding on preferred foods of brent geese (Nyholm 1965, Charman and Macey 1978, Charman 1979, Reed

et al. 1998a, Ganter 2000). The number of short-time stopovers and their duration varied considerably among individuals, from 1 to 11 stopovers and from 4 to 111 hours spent on stops (Appendix 2).

The birds with summer destinations on Svalbard made 1–5 stopovers in terrestrial habitats in the southwestern or central parts of Spitsbergen (birds E, F, G, H, J and K) or on Edgeøya (bird A, Fig. 3), before arriving at their breeding or moulting site. More than half of these stopovers had durations of > 48 hours and were classified as long-time stopovers (Appendix 3). The birds C and D migrating to Greenland in 1997 only made a short-time stopover in terrestrial habitats west of Kap Eilar Rasmussen in easternmost Peary

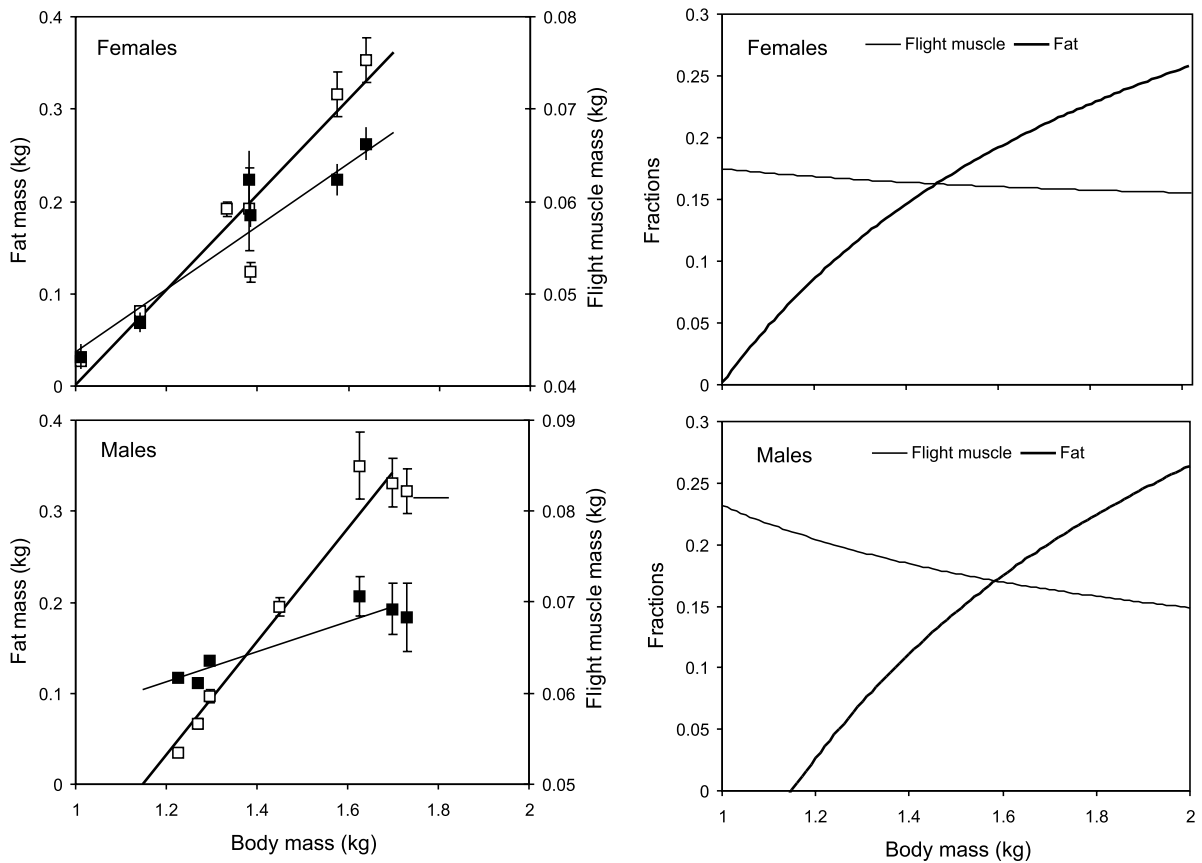


Fig. 2. Body composition of male and female brent geese in relation to their body mass. In the diagrams to the left, open symbols gives average values \pm SE for fat content, and the solid lines the estimated regression lines. Females: dry fat (in kg) = $0.5147 \times$ body mass (in kg) $- 0.5129$ ($R^2 = 0.77$), and for males: dry fat (in kg) = $0.6204 \times$ body mass (in kg) $- 0.7127$ ($R^2 = 0.84$). Closed symbols gives average values \pm SE for dry-mass flight-muscle mass, and the thin lines the estimated regression lines. For females: dry flight-muscle mass (in kg) = $0.0339 \times$ body mass (in kg) $+ 0.0098$ ($R^2 = 0.65$), and for males: dry flight-muscle mass (in kg) = $0.0164 \times$ body mass (in kg) $+ 0.0416$ ($R^2 = 0.26$). The diagrams to the right present the regression lines recalculated to fractions of the total body mass. Note that the fractions for flight-muscle are based on wet weight, assuming this to be four times the dry weight.

Land, before flying to Kilen (Clausen and Bustnes 1998, Fig. 3, Appendix 3). Bird I moving via Svalbard in 2001 made three short-time stopovers in terrestrial habitats on the west coast of Spitsbergen, before migrating to Kilen (Fig. 3, Appendix 3).

Estimated flight distances for the first long-distance flight from Denmark to the first destination in Svalbard or Greenland averaged 2557 km (range 2374–3243 km) or 2762 km (range 2436–3366 km), based on short and long estimates, respectively (Appendix 2). Bird I added another 637–723 km when migrating from Svalbard to Greenland (leg 2, Appendix 2). All birds (except B, for which we have no data from that part of the track) flew around the southwestern part of Norway instead of flying over it, and some birds (especially birds B and H) made quite long detours when crossing the Norwegian and Barents Seas, in

contrast to others (birds E, F, I and K) who made fairly straight flights over sea (Fig. 3). Most birds therefore flew 5–15% longer distance than along the perfect orthodrome routes between Denmark and their first destinations in the Arctic (compare Fig. 3 and 4, Appendix 2), but bird B probably added 48% and bird H added 17–24% (Appendix 2).

In addition to these long-distance flights the birds flew on average 223 km (range 138–355 km) on short-distance flights between stopovers in the Arctic before arriving at their final summer destination (Appendix 3). Combining data from Appendixes 2 and 3 gives the total flight range from Denmark to the final summer destination, averaging 2849 km (range 2560–3440 km, $n = 9$, excluding bird B) or 3057 km (range 2728–3607 km, $n = 10$, including bird B), based on short and long estimates from Appendix 2, respectively.

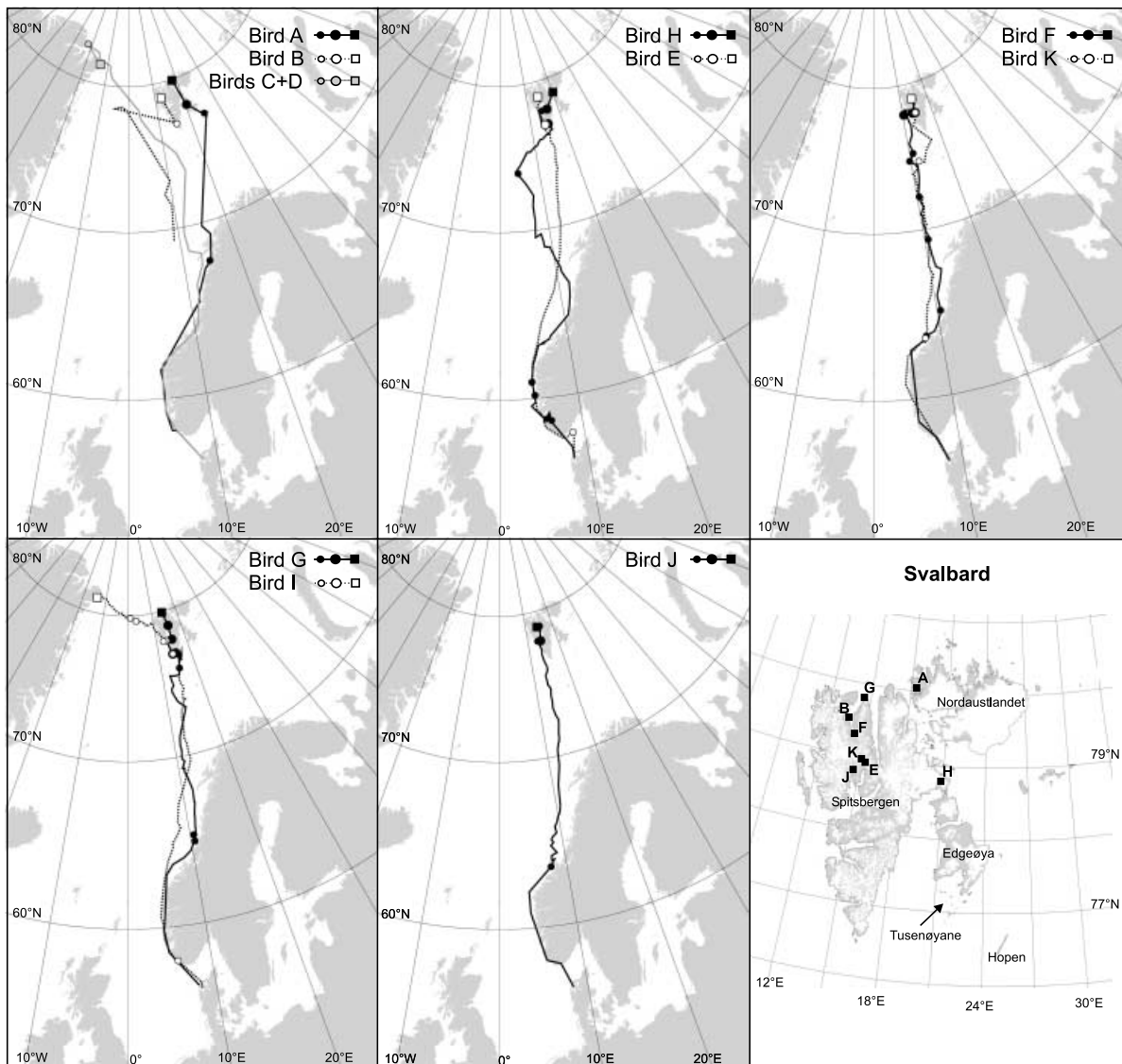


Fig. 3. Trackings of light-bellied brent geese with satellite-telemetry, late May and early June, 1997 and 2001. Small dots and large dots gives short-time and long-time stopovers, respectively, while quadrats gives the final summer destination (defined as location on 15 June). Bird B was only tracked on part of the flight (Clausen and Bustnes 1998). Maps with trackings are in gnomonic projections. The inserted map of Svalbard gives names and locations of islands mentioned in the text, and the final summer destinations of birds summering in Svalbard (identified by letters).

Predicted maximum flight ranges versus observed distances

Estimated maximum flight ranges based on the software of Pennycuik (2002, Table 1) were on average 3716 km (sd = 601 km, range 1957–4654 km, n = 18) for males, and 3345 km (sd = 255 km, range 2625–3646 km, n = 15) for females (Fig. 5). Thus, all birds (except one exceptionally thin male) were predicted to easily reach Svalbard (ca 2400–2600 km), but only 14–16 of the 18 males and 7–12 of the 15 females were predicted to reach Greenland (ca 3300–3500 km). Among the

birds with known flights, i.e. birds with satellite transmitters or associated mates, one out of 10 males probably, and two out of six females certainly flew longer than predicted by the model (Fig. 6).

Female nutrient stores on arrival at the breeding grounds

In Fig. 7 we illustrate the estimated changes in body composition of two females who were paired to transmitter-birds, and who flew to Svalbard (ring code

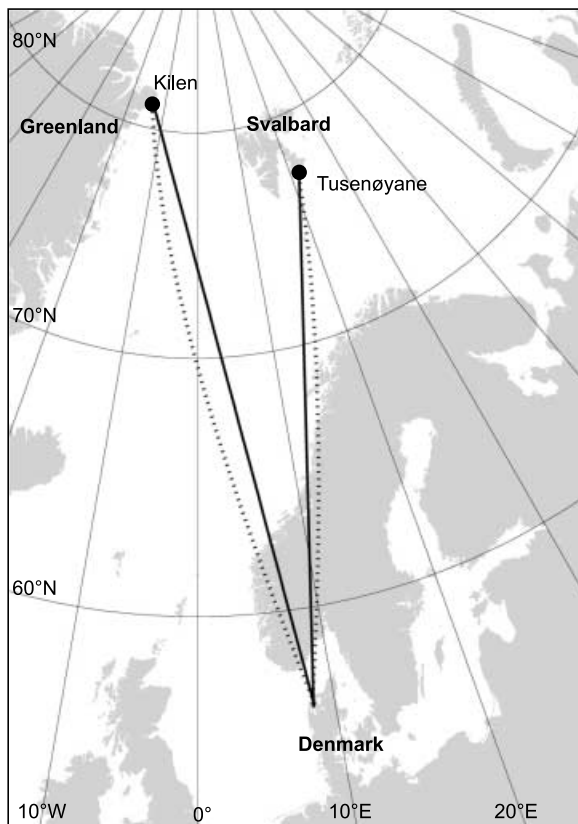


Fig. 4. Orthodromes (thick solid lines) and loxodromes (thick dotted lines) from the spring staging area in northwestern Denmark to the two main breeding areas of the studied brent goose population, Tusenøyane in southeastern Svalbard and Kilen in northern Greenland. The map is in a gnomonic projection.

WLYY, mate of bird F) and Greenland (WOYF, mate of bird I), respectively, in relation to estimated breeding costs, in terms of fat and protein needed to lay an average clutch and incubate it. Both birds would arrive

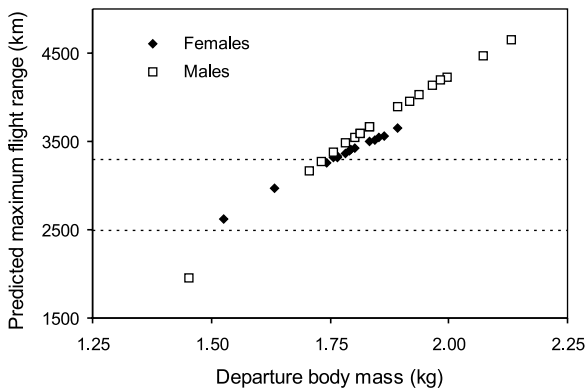


Fig. 5. Predicted maximum flight ranges of male and female light-bellied brent geese in relation to their estimated departure body masses. The two dotted lines indicate arrival to Greenland (upper) and Svalbard (lower), respectively.

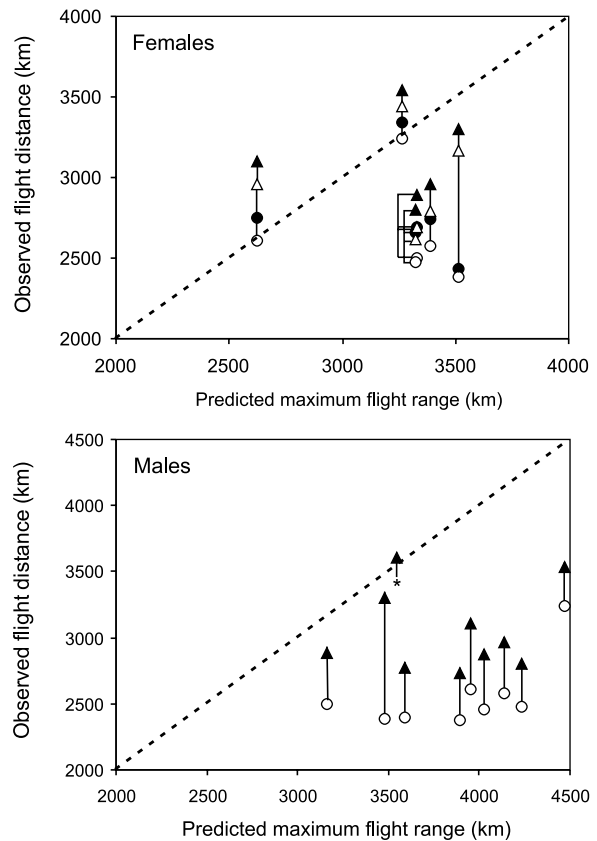


Fig. 6. Observed flight distances of satellite tracked birds (or associated females) plotted against predicted maximum flight ranges of the same individual. For each bird several observed flight distances indicated by different symbols are shown, joined by lines. The dots give the range of the first oceanic long-distance flight, without any long-time stopovers (from Appendix 2). The triangles give the range to the final summer destination, including all flights and stopovers (from Appendixes 2 and 3 combined). Filled symbols are based on the long estimates and open symbols on the short estimates in Appendix 2, respectively. For males only the shortest and longest estimate of observed flight range are given. The hatched line indicates $y = x$, observed flights above this line are longer than predicted maximum flight ranges. The star indicates a male for which the shortest flight not could be estimated (too few data).

with surplus supplies of protein, because this could be derived either from subsequent atrophy of flight muscles or proteinaceous airframe components (e.g. from leg muscles, gizzard or liver, Ankney and MacInnes 1978, Ankney 1984, Fig. 7). The Svalbard-destined bird, which departed with an estimated body-mass of 1.77 kg would also arrive with most of the fat needed for reproduction (Fig. 7). Estimated fat carried from Denmark to Svalbard is 42 g if migrating 2889 km (longest estimate of 2693 km in Appendix 2 + 196 km of local movements on Svalbard from Appendix 3) – or 62 g if migrating 2693 km (shortest estimate of 2497 km in Appendix 2 + 196 km of local movements on Svalbard from Appendix 3). The Greenland-destined bird,

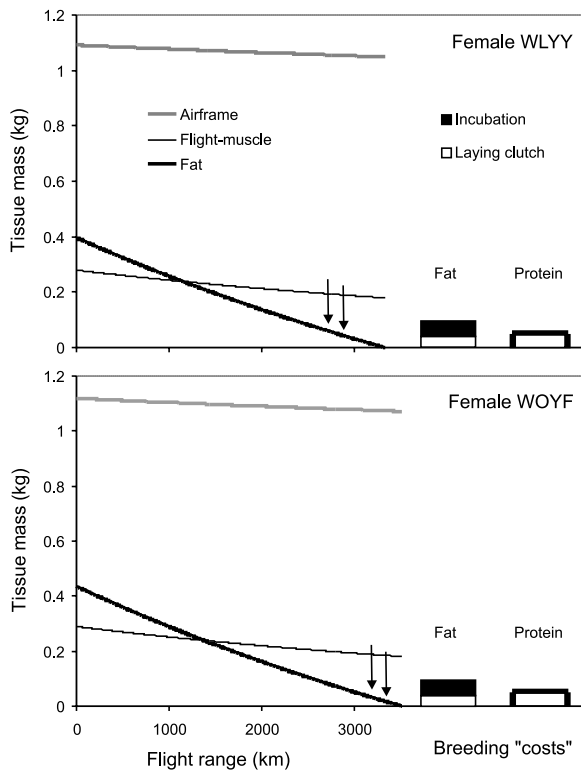


Fig. 7. Estimated changes in body composition of two females paired to transmitter-marked male brent geese migrating to Svalbard (WLYY mate of bird F) and Greenland (WOYF, mate of bird I) in 2001. The body is divided in three components: fat, flight-muscle and the airframe (i.e. the rest of the birds), all in wet masses. The small arrows indicate the flight range actually covered by the birds, with the short estimate below the left and the long estimate below the right arrow, respectively. The bars at the right side of the figures give estimates of needed resources of fat and protein if the birds were to lay an average clutch and incubate it. The average clutch of brent geese from the studied population is 3.86 (average from 4 yr, Nyholm 1965, Madsen et al. 1989, J. Madsen and P. Clausen, unpubl.), and the egg mass is 80.4 g (wet mass; 11 eggs from 3 clutches, excluding a very small egg, Nyholm 1965), giving a total clutch mass of 310.6 g (wet mass). Assuming composition similar to cackling Canada geese *Branta canadensis minima* Ridgway (Raveling 1979), 12.7% or 39.4 g is fat and 14.8% or 46.0 g is protein (wet masses). Incubation costs is taken from Ankney (1984), who found that female brent geese during incubation lost 54.5 g fat and 3.3 g (dry) protein, equivalent to 13.2 g wet protein. In these calculations we assume that ratios between dry:wet masses are 1:1 for fat, and 1:4 for protein, respectively (Raveling 1979, Ankney 1984).

departing on 30 May with a body-mass of 1.84 kg, would have less fat left. Estimated fat carried from Denmark to Greenland is 21 g if migrating 3301 km (longest estimate of 2436 km for leg 1 and 723 km for leg 2 in Appendix 2 + 142 km of local movements on Svalbard from Appendix 3) – or 34 g if migrating 3166 km (shortest estimate of 2387 km for leg 1 and 637 km for leg 2 in Appendix 2 + 142 km of local movements on Svalbard from Appendix 3). The interpretation of

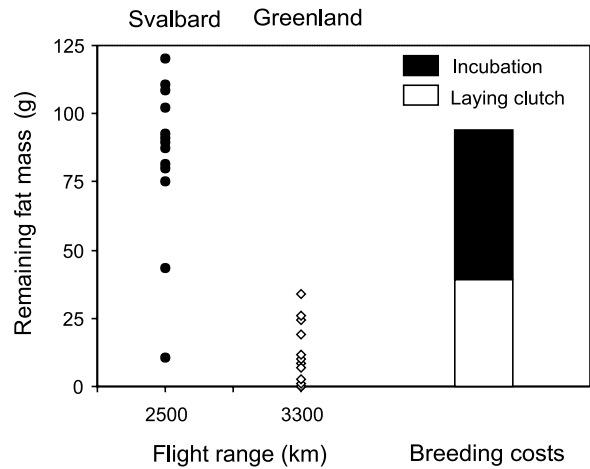


Fig. 8. Estimated stores of fat of 13 female brent geese after a flight to Svalbard (ca 2500 km) and Greenland (ca 3300 km), respectively. The birds included are all studied females except WLYY and WOYF for which a more comprehensive analysis is given in Fig. 7. The bars at the right side of the figure give estimates of needed resources of fat if the birds were to lay an average clutch and incubate it (details, see Fig. 7).

these results is that the Svalbard-destined bird is barely capable of laying and incubating an average clutch, based on body-stores carried from spring staging areas in Denmark. In contrast the Greenland-destined bird must either reduce the clutch or rely on exogenous resources for incubation costs.

The same conclusion followed from the computations for the other females. Most would have sufficient fat-stores left when arriving to Svalbard, but only few would have sufficient fat-stores to both lay and incubate an average clutch if migrating to Greenland (Fig. 8). Females flying to both destinations would have sufficient protein-stores (data not shown).

Breeding output

All birds followed by satellite telemetry in 1997 returned without goslings (Clausen and Bustnes 1998). The same happened in 2001, except for the pair composed of bird I and female WOYF, which returned with at least one gosling from their breeding site in Kilen, Greenland. This may seem to indicate a negative impact of the transmitters on the birds, but the female returning with a gosling was the one with a poor likelihood of successful breeding (Fig. 7). In 1997 the breeding success in the population as a whole was rather good, with 18.9% juveniles, but despite this only an estimated 23.5% of the potential breeders in the population returned with goslings (Clausen and Bustnes 1998). In 2001 breeding success was poor, with 6.8% juveniles ($n = 3037$ sampled individuals).

Discussion

Predicted maximum flight ranges, observed flight distances and detours

The predicted maximum flight ranges suggest that the studied geese generally would have no problems with flying to breeding locations on Svalbard, but that several birds would barely be able to fly to breeding locations in Greenland (Fig. 5). Two of the tracked birds flew distances similar to maximum flight ranges if we use the shortest estimate of travelled distances, and flew considerably longer than the model predicted they would be able to do if we use the longest estimate (Fig. 6). We believe that the long distance estimate is closest to reality, because the short estimate is based on fewer locations, and this in several cases leads to flight routes significantly different from the general picture of the flights of all birds combined. The shortest estimates for some birds thus incorporates flights across southwestern Norway, a situation not evident from any of the satellite-tracked birds for which we have high accuracy locations on that part of the track. It is neither evident from field observations in Norway, showing that the majority of brent geese take the coastal route (M. Green, unpubl.). By taking the detour around southwestern Norway the birds add a few hundred kilometres, but avoid having to climb >1500 m above sea-level to make the journey, a known hazard to migrating brent geese (Gudmundsson et al. 1995). Apart from this detour, the tracked birds, with two exceptions (B and H), generally made fairly direct flights to the Arctic, adding less than 15% to a perfect orthodromic flight directly from Denmark to their first Arctic destination.

Body stores remaining upon arrival and the capital breeding hypothesis

Our analysis of remaining body stores of fat and protein in females showed that the birds generally were predicted to arrive to Svalbard with good supplies of both fat and protein, but not in Greenland, where most birds would arrive almost lean of fat (Fig. 7 and 8). Ankney (1984) demonstrated that brent geese breeding at rather low latitude (Southampton Island, 64°N) were partly dependent on endogenous stores of especially fat, but also protein to lay and incubate their eggs. Our study birds breed considerably further north – on Svalbard (77–80°N, Mehlum 1998) and in Greenland (81°N, Hjort 1995). This mean that birds from our study population are facing shorter growing seasons than the brent geese on Southampton Island – and therefore probably have to initiate their clutches within a shorter interval after arrival. Failing to initiate breeding immediately after arrival to the breeding ground

probably has major negative fitness implications for the birds. It is known that late hatched goslings of most studied Arctic goose populations have slower growth rates, and fledge with lower structural body size (reviewed by Cooch 2002). Sedinger and Flint (1991) demonstrated that this also applies to brent geese, and Sedinger et al. (1995) found that late hatched and smaller goslings survived less, recruited later to the breeding population and laid smaller eggs later in their lives.

In view of this it seems reasonable to assume that endogenous requirements for breeding are at least as important to brent geese in Svalbard and Greenland, as it was in Southampton Island. We therefore used data from Svalbard on egg masses (Nyholm 1965) and clutch sizes (Nyholm 1965, Madsen et al. 1989, Clausen et al. 1999) to predict the minimum requirements of endogenous stores needed for a successful breeding attempt of brent geese from our study population. Fig. 7 and 8 indicate that birds have fair chances of breeding in Svalbard, but breeding in Greenland as they do seems impossible. As outlined in the introduction, about 20% of the east Atlantic flyway-population of light-bellied brent geese migrate to Greenland. This proportion has apparently remained constant between 1985 and 1998, and the growth rate of the Greenland sub-population seems to be just as good as that of the Svalbard sub-population, despite the added flight distance of ca 700–1000 km. This leaves us with the question how the brent geese can manage the flights to northern Greenland, and still be able to breed there?

Is the predicted fuel consumption during flight realistic?

Is there a risk, that the calculations of the birds fuel use and of remaining body-stores are misleading – simply because the model is wrong? Pennycuick's (1975) mechanical flight model has been subject of much discussion. For example, it is claimed that it makes too low predictions about maximum flight ranges of birds migrating in still air, and several alternative flight metabolism models have been published (Greenevald 1975, Summers and Waltner 1979, Davidson 1984). We discard the idea of the poor model for the time being, because several essential default parameters of the original version have been changed significantly in the last few years (Pennycuick 1995, 1998, 2001, Pennycuick et al. 1996a), and model outputs seem fairly consistent with actually observed flight performance and/or body-store changes in birds (Pennycuick 1998, 2001, Pennycuick and Battley 2003). We measured the wing-span and-area on only two dead birds and assumed these to be representative for all birds studied. This method may be considered inappropriate, but our estimated values for the free-living birds in fact are very similar to a

sample of 20 brent geese of the same sub-species measured in Iceland (Gudmundsson et al. 1995). On this background we also consider the input values for wing morphometrics as adequate.

Are the estimated departure body masses too low?

A crucial estimate is that of the departure body mass. This was estimated by combining body mass at capture with an estimate of mass gained between capture and departure from abdominal profile index increments. The estimated body mass increments were 5.45 g/day in 1997 and 3.79 g/day in 2001, respectively. The brent geese at Agerø and Mågerødde are primarily feeding on saltmarshes and occasionally switch to feeding on *Zostera marina* L. beds (Clausen 1998). Daily body mass increments of spring feeding brent geese on saltmarsh habitats in the Wadden Sea region have frequently been addressed. Ebbinge (1989) gives daily increments of 10 g/day, and Stock and Hofeditz (1997) give a range from 11.1–11.9 g/day. Prop and Deerenberg (1991) studied the spring fattening of brent geese on Dutch saltmarshes in more detail and found daily body mass increments ranging from 2–10.2 g. They, however, pointed out that the high values for fattening rates were for birds feeding on highly nutritious halophytes such as *Plantago maritima* L. and *Triglochin maritimum* L., that fattening rates declined in the second half of May, and that birds feeding on a poorer *Puccinellia*-dominated diet might have to cope with fattening rates below 4 g/day. Clausen (1998) found that the brent geese around Agerø, to a much higher degree than those studied by Prop and Deerenberg (1991), were feeding on *Festuca/Juncus* and *Puccinellia*-dominated marshes without the nutritious halophytes, suggesting a poorer spring-fattening potential of these marshes. In conclusion, our estimates of body mass increments seem reasonable, although we cannot exclude that some birds might have been departing with 50–75 g extra body mass (adding 5 g extra per day during 10–15 days staging after capture). A mass increment of this magnitude would change the predictions so that most birds could reach Greenland, but a majority would still arrive with too small fat stores for breeding.

The poor breeding output in the whole flyway-population in the main study year, 2001, could be indicative of a poor spring fattening year (Ebbinge and Spaans 1995). We exclude this interpretation, because neither body mass of captured birds, nor abdominal profile index measurements, nor the meteorological conditions in 2001 indicate an exceptionally cold, warm, wet or dry year. The average temperature for April–May 2001 was 8.5°C (normal 1961–1990 was 8.25°) and cumulative precipitation was 118 mm (normal 1961–1990 was 89 mm, data from the Danish Meteorological Institute monthly reports). All four

weather scenarios are known to cause poor fattening conditions (Prop and Deerenberg 1991, Clausen 1998). The poor breeding success must therefore be a result of factors affecting the birds on their spring migration – or in the breeding areas.

Towards solving the discrepancy between model predictions and the reality

We recognise four major hypotheses which alone, or in combination, might solve how brent geese manage to breed in Greenland, and highlight these as major research challenges for the future.

Refuelling stopovers

Our analysis of remaining fat and protein stores upon arrival does not take into account the significance of refuelling stopovers in Spitsbergen. All birds destined for Svalbard spent several days feeding in stopover sites before moving to their final summer destination, but this behaviour is in contrast to the three birds we tracked to Greenland, which spent less than 2 days on short-time stopovers. From these few focal birds we can, however, not exclude that many more birds in some years migrate via Spitsbergen to Greenland. The light-bellied brent geese usually depart from Denmark in the last 10 days of May (Clausen et al. 1998). If we assume the brent geese in Greenland initiate laying at the same time as those breeding in Svalbard (median date 10 June, Madsen et al. 1989), some of them could spend 10–15 days refuelling on the west coast of Spitsbergen. The route is probably known to Greenland breeders generally, as the satellite trackings in 1997 and 2001 demonstrated that the Greenland birds migrate via Spitsbergen on return migration and spend several days refuelling there (Clausen and Bustnes 1998, P. Clausen, M. Green and T. Alerstam, unpubl.).

Field studies of individually marked brent geese and their feeding ecology and energetics at stopover sites in west-Spitsbergen will enable us to understand the significance of these sites as refuelling stopovers.

Wind assistance

The calculations were based on the assumption that the birds migrate in still air. However, it is evident that Canada geese *Branta canadensis* (L.) tend to depart under favourable tail-winds and adjust their migratory behaviour in relation to wind conditions to save energy (Wege and Raveling 1983, 1984). Dark-bellied brent geese generally also depart during favourable tail-winds (Green 1998, Green et al. 2002), and Ebbinge (1989) found that breeding success of dark-bellied brent geese was depressed in years where they had been migrating against head-winds over the Baltic Sea. Dau (1992) studied the autumn migration of Pacific black brant *Branta bernicla nigricans* (Lawrence), which make a non-stop 4400–5300 km transoceanic flight from

Alaska to wintering sites in Mexico. He pointed out that for the geese to make this journey, they probably had to fly at ground-speeds of ca 100 km/hour by using favourable tail-winds associated with specific weather situations. If wing morphometrics of black brant are comparable to those of light-bellied brent geese, our computations of maximum flight ranges strongly support his interpretation, because departure masses of black brants and our study birds are very similar (Dau 1992, Reed et al. 1998a). The black brant safe-guard sufficient body stores for breeding by having a distinctly different migratory strategy in spring, where they use several stopovers on the Pacific coasts of lower USA, Canada and Alaska to fuel their return flight to the breeding areas (Einarsen 1965, Wilson and Atkinson 1995, Reed et al. 1998b).

We know from observations in Denmark that the light-bellied brent geese we study in most years also depart on days with no wind or tail-winds. Nevertheless, as pointed out by Pennycuick et al. (1996b), who studied migrating whooper swans *Cygnus cygnus* L. by satellite telemetry, favourable departure winds do not necessarily imply that favourable winds prevail on the whole journey. To assess the importance of wind-assistance for spring migrating light-bellied brent geese we need an analysis of departure dates and wind-conditions for the whole flight, an analysis beyond the scope of this paper.

Formation flights

Lissaman and Scollenberger (1970) and Hummel (1973, 1978) highlighted the theoretical significance of formation flight as a means by which migrating birds could save energy. Cutts and Speakman (1994) and Speakman and Banks (1998) studied formation flights of pink-footed geese *Anser brachyrhynchus* and greylag geese *Anser anser*, respectively. Their analyses suggest that the former might save 2.7–5.5% and the latter 4.5–9.9% in total flight cost by flying in formation. Recent studies on white pelicans *Pelecanus onocrotalus* using heart rate measurements to estimate energy expenditure found a reduction in cost of flight of 1.7–3.4% due to formation flight (Weimerskirch et al. 2001).

Brent geese fly in formations similar to the ones found in larger geese and pelicans, even though the large flocks formed during migration may consist of several smaller formations, making the formation flight less obvious than in the larger species (M. Green, pers. obs.).

Flying without guts

A final possibility of energy-saving is that of birds 'flying without guts'. Some grebes and waders reduce the size of their digestive organs before long-distance migrations (Jehl 1997, Piersma and Lindström 1997, Piersma and Gill 1998). They use the nutrients mo-

bilised by catabolism of the digestive system to build larger pectoral muscles, thereby improving their flight capabilities and fuel-stores that can be used during long-distance flights. This atrophy of digestive organs can occur within a few days (Gaunt et al. 1990, Piersma et al. 1999). If the brent geese do the same, this means that the fraction of the body mass that constitutes the 'airframe components' would be reduced. At the same time the fat and flight-muscle fractions would increase, enabling the birds to fly a longer distance with the same body mass (Pennycuick and Battley 2003).

However, as pointed out by Clausen et al. (2002) the meagre evidence available suggest that pronounced premigratory atrophy of the intestinal system is not very important among waterfowl (Clausen et al. 2002), although Gauthier et al. (1984) demonstrated that female greater snow geese *Chen caerulescens atlanticus* L. at one of two study sites did reduce stomach mass prior to a long-distance movement. Reducing the stomach will, however, lower the digestive capacity of the birds, because they lose some of their grinding capacity. The waders cope with this by switching from feeding on hard-shelled food items (such as molluscs and leather-jackets) to soft-bodied (polychaete worms, Piersma et al. 1993). Snow geese differ from brent geese in their feeding behaviour, and often feed by grubbing for easily digestible below-ground tillers, rhizomes and roots (Gauthier 1993, Belanger and Bedard 1994, Carriere et al. 1999). In contrast, this feeding behaviour is not known from any studies of brent geese in terrestrial habitats, probably because the smaller brent geese have a bill adapted for pecking on above-ground rather than grubbing for below-ground parts of plants. Feeding on above-ground parts would normally imply that the birds also feed on a material with higher fibre content (Mathers and Montgomery 1996, Nolet et al. 2001), and for that reason require longer intestines and larger caecae to be digested (Clench and Mathias 1995, MacWilliams and Karasov 2001). Atrophy of the digestive system prior to migration would thus partly counteract the refuelling capability of the brent geese if they feed in terrestrial habitats. Most of the brent geese tracked by satellite telemetry migrated to terrestrial refuelling stopovers before arriving to their final summer destinations. This suggest that the brent geese do need a full digestive capacity when arriving in the Arctic – and that gut atrophy may be a less likely hypothesis that can explain the discrepancy between observed flight distances and the birds need for stores that can be invested in breeding.

In conclusion, we believe that the first three mentioned hypotheses – additional refuelling in the Arctic, wind assistance and formation flight are the most important means by which the brent geese can manage to breed in Greenland.

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Appendix 1. Body masses and estimated fat, flight-muscle and airframe fractions of 27 brent geese studied during May 1997 and 2001. Mass gain gives the estimated body mass change between capture and departure of the birds. Transmitter birds are noticed.

BirdID	Transmitter birds	Body masses (kg)			Fractions		
		At capture m_{capture}	Mass gain m_{change}	At departure $m_{\text{departure}}$	Fat	Flight-muscle	Airframe
Females							
RBL	C	1.66	0.082	1.74	0.220	0.158	0.622
RAF		1.71	0.082	1.79	0.228	0.158	0.614
RAL		1.81	0.082	1.89	0.244	0.156	0.600
WOYJ		1.49	0.036	1.53	0.179	0.161	0.660
WLYY		1.73	0.036	1.77	0.224	0.158	0.618
WPYL		1.58	0.053	1.63	0.201	0.160	0.640
WOYP		1.71	0.053	1.76	0.223	0.158	0.619
WJYT		1.73	0.036	1.77	0.224	0.158	0.618
WJYY		1.73	0.053	1.73	0.227	0.158	0.615
WOYB		1.74	0.053	1.73	0.229	0.158	0.614
WOYH		1.75	0.053	1.80	0.230	0.157	0.612
WNYH		1.78	0.053	1.83	0.235	0.157	0.608
WOYF		1.79	0.053	1.84	0.236	0.157	0.607
WPYP		1.80	0.053	1.85	0.238	0.157	0.605
WPYT		1.81	0.053	1.86	0.239	0.157	0.604
Average female		1.72		1.78	0.225	0.158	0.617
Males							
RAU		1.37	0.082	1.45	0.130	0.180	0.690
RAP	B	1.72	0.082	1.80	0.225	0.158	0.617
RAV	A	1.89	0.082	1.97	0.258	0.150	0.592
RAS	D	1.99	0.082	2.07	0.276	0.146	0.578
WLYT	F	1.67	0.036	1.71	0.203	0.163	0.634
WPYN	J	1.86	0.036	1.89	0.244	0.154	0.603
WOYN	H	1.88	0.036	1.92	0.248	0.152	0.599
WNYJ	G	1.90	0.036	1.94	0.252	0.152	0.596
WPYY	K	1.96	0.036	2.00	0.263	0.149	0.588
WOYO	I	1.73	0.053	1.78	0.221	0.159	0.620
WNYF	E	1.76	0.053	1.81	0.227	0.157	0.615
WHYY		1.68	0.053	1.73	0.209	0.162	0.629
WPYS		1.71	0.053	1.76	0.215	0.160	0.625
WFYY		1.76	0.053	1.81	0.227	0.157	0.615
WPYO		1.78	0.053	1.83	0.232	0.156	0.612
WNYB		1.78	0.053	1.83	0.232	0.156	0.612
WPYJ		1.93	0.053	1.98	0.261	0.149	0.589
WOYS		2.08	0.053	2.13	0.286	0.144	0.570
Average male		1.80		1.86	0.234	0.156	0.610

Appendix 2. Long-distance (oceanic) migrations, stopover site use, and detour flights of light-bellied brent geese followed by satellite telemetry, 15 May–15 June, 1997 (birds A to D) and 2001 (birds E to K). All birds except C are males. For each bird associated mates (ringcodes, if mates caught and subsequently identified in the field) is noticed – UNR means bird having a mate without rings.

Bird ID	Note	Mate	Departure date	Arrival date	Travelled distance		Total travel time hours	Flight time hours	Stopover time hours	No. of stopovers		Detours	
					shortest ¹ estimate km (tracks)	longest ² estimate km (tracks)				>48 hours	<48 hours	Direct orthodrome distance km	detour% ⁸
A		R_AF	30 May	2 or 3 June	2578 (3)	2744 (14)	83 ⁵ (103) ⁶	59	24 ⁵ (44) ⁶	0	2	2419	6.6–13.4
B			29 May (?)	2 June	n.a. ³	3366 ⁴ (15)	n.a.	n.a.	n.a.	n.a.	n.a.	2268	n.a. 48.4
C and D	paired		30 May	2 June	3243 (5)	3341 (24)	88	69	19	0	1	2874	12.8–16.2
E		UNR	30 May	1 June	2393 (9)	2534 (31)	48	44	4	0	1	2268	5.5–11.7
F		WLYY	25 May	28 May	2497 (16)	2693 (36)	68	40	28	0	6	2410	3.6–11.7
G		UNR ¹⁰	25 May	28 May	2460 (17)	2553 (35)	62	43	19	0	3	2218	10.9–15.1
H		WOYJ	25 May	1 June	2606 (20)	2748 (44)	165	54	111	0	11	2218	17.5–23.9
I	1 leg ⁷ 2 leg ⁷	WOYF	30 May	1 June	2387 (22)	2436 (44)	50	44	6	0	1	2234	6.8–9.0
			4 June	5 June	637 (8)	723 (17)	25	15	10	0	2	611	4.2–18.3
J		UNR	26 May	28 May	2374 (12)	2542 (32)	66	42	24	0	1	2302	3.1–10.4
K		WJYT ¹⁰	25 May	29 May	2477 (19)	2661 (40)	81	49	32	0	0	2331	6.3–14.2
Average ⁹					2557 ⁹	2762 ⁹							

¹This estimate is the shortest possible flight, flying along orthodromes between locations of high quality (ARGOS classes 1,2,3). ²This estimate is the distance of tracks presented in Fig. 3, based on flights along loxodromes between selected locations (ARGOS classes 3,2,1,0,A; in 1997 also B). ³To few ARGOS location class 3,2,1 positions to make an estimate. ⁴No locations of first half of flight, estimate based on assumption that Bird B flew same route as birds C and D from Denmark to Vega in mid-western Norway (further details in Clausen and Bustnes 1998). ⁵Assuming that the bird left the Hopen-area directly after the last position was received and made a direct flight to Edgeøya. ⁶Assuming that the bird had just arrived at Edgeøya when the first position was received from there. ⁷1 leg describes the migration from Denmark to Svalbard, 2 leg from Svalbard to Greenland (Fig. 3). ⁸The two values gives added flight distances in % of direct orthodrome distances relative to travelled distances for shortest and longest estimates, respectively. ⁹Excluding 2nd leg of bird I. ¹⁰This mate was identified during spring 2002 – it is assumed the birds also were paired in 2001 (brent geese have long duration pair bonds, Ebbing 1992).

Appendix 3. Short-distance migrations and stopover site use of light-bellied brent geese followed by satellite telemetry, 15 May–15 June, 1997 and 2001, and after having arrived to Svalbard or Greenland.

Bird ID	Arrival on summer location Date	Travelled distance ¹ km (tracks)	Total travel time hours	Flight time ² hours	Stopover time hours	No. of stopovers	
						>48 hours	<48 hours
A	7 June ³ (8 June)	217 (1)	103 ³ (125)	3	100 ³ (122)	1	0
B	11 June	122 (2)	241	2	240	1	1
C and D	4 June ³ (4 June)	197 (1)	32 ³ (43)	3	29 ³ (40)	0	1
E	4 June	241 (4)	65	4	61	1	0
F	11 June	196 (4)	333	3	330	3	1
G	12 June	318 (6)	363	5	358	4	1
H	13 June ³ (19 June)	355 (7)	271 ³ (433)	6	265 ³ (427)	2	2
I	n.a. ⁴	142 (2)	62	2	60	0	3
J	11 June	186 (6)	321	3	318	2	2
K	5 June	138 (19)	176	2	174	1	1
Averages		223					

¹This estimate is the shortest possible flight, flying along orthodromes between stopover sites, and only using locations of high quality (ARGOS classes 1,2,3 in 2001, also 0 in 1997) during flights; the number of tracks is thus the number of orthodromes calculated. ²Flight time not necessarily exactly known, calculated from travelled distance assuming speed of 18 m/sec, and rounded to nearest full hour. ³Exact departure from last stopover site and arrival to summer site not known (transmitter turned OFF). The estimate gives time if assuming bird left last stopover site immediately after we received a satellite location from the site, the estimate in () if assuming bird had just arrived on the summer site immediately before we received a satellite location from the site. ⁴Data for this bird refers to its use of stopovers on Svalbard, before continuing to Greenland. Arrival on Greenland is given in Appendix 2, Bird I leg 2.