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Dark-bellied Brent Geese *Branta bernicla bernicla*, as recorded by satellite telemetry, do not minimize flight distance during spring migration

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Nine Dark-bellied Brent Geese *Branta bernicla bernicla* were equipped with satellite transmitters during spring staging in the Dutch Wadden Sea in 1998 and 1999. The transmitters (in all cases less than 3% of body mass) were attached to the back by a flexible elastic harness. One juvenile female was tracked to the Yamal peninsula in 1998. Eight adult males were selected from a single catch of 75 to span the range of body mass observed on the date of capture (11 May 1999) and all but the lightest individual completed the first lap of the migratory flight to the White Sea, Russia, according to the time schedule normal for the species. Six birds were successfully tracked to Taymyr for a total distance averaging 5004 km (range 4577–5164) but judging from later movements none bred (although 1999 was a breeding year). Although the routes chosen during spring migration were closely similar, none of the tagged birds migrated together. On average the geese used 16 flights to reach their summer destinations on Taymyr. The longest uninterrupted flights during the first half of the journey (Wadden Sea to Kanin) covered 1056 km (mean of seven adult males, range 768–1331), while the corresponding value for the second half of the migration (Kanin–Taymyr) was only 555 km (mean of six adult males). Only 7% of total time during spring migration was spent in active flight, as contrasted to *c.* 80% at long-term stopovers. Overall average travelling speed was 118 km/day (range 97–148). Including fattening prior to departure the rate of travel falls to 62 km/day (range 49–70), in keeping with theoretical predictions. Routes followed deviated from the great circle route, adding at least 700 km (16%) to the journey from Wadden Sea to Taymyr, and we conclude that the coastal route is chosen to facilitate feeding, drinking and resting en route instead of minimizing total flight distance.

The ability to follow an individual migratory bird in detail from wintering to breeding quarters did not exist until miniature satellite transmitters became available. During the last 15 years several satellite telemetry studies have been conducted on larger seabirds, storks, swans, geese and raptors (Fuller *et al.* 1995, Beekman *et al.* 1996). Although many of these studies have concentrated on discovering wintering or feeding areas, researchers are increasingly using the technique to study migratory behaviour, for example to ask how birds conduct their migrations, how long are the flights between stopovers, where and for how long do they stop to refuel, whether their migratory routes follow great circles (orthodromes) or constant geographical courses (loxodromes), and what are the overall migratory speeds reached by the birds.

The Dark-bellied Brent Goose *Branta bernicla bernicla* (hereafter Brent) is a well-studied species and the large-scale patterns of spring migration are fairly well known (Cramp & Simmons 1977, Bergmann *et al.* 1994, Green 1998). The birds leave their wintering areas in Britain and France during March–early April and the whole population gathers in the Wadden Sea (Netherlands, Germany, Denmark) for spring staging in April–May. They leave this area in late May

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for an assumed non-stop flight to their next main staging area in the White Sea, north-west Russia. After 2–3 weeks they continue north-east. Mass arrival at the breeding grounds at Taymyr usually takes place between 10 and 20 June (Spaans *et al*. 1998).

Although the overall patterns regarding routes and timing of migration are known, there still remain large gaps in our knowledge about how individual birds conduct the migration in detail. To fill these gaps we equipped Brent with satellite transmitters during 1998–1999. An energetic reconstruction of spring migration will be given in a companion paper.

METHODS

During 1998 and 1999 we equipped nine Brent with Microwave Telemetry Inc. PTTs (Platform Transmitter Terminals) during spring staging in the Netherlands. The geese were caught by cannon net on the islands Schiermonnikoog (53°29′N, 6°13′E) and Terschelling (53°26′N, 5°30′E) in the Wadden Sea. On 14 May 1998 one juvenile female, from a catch of two birds, was supplied with a specially manufactured 22-g PTT (1.6% of the bird's body mass) on Schiermonnikoog. The transmitter was the standard Microwave 20-g device but with a heavier antenna from the standard 30-g PTT. On 11 May 1999 eight adult males, from a catch of 75 birds, were equipped with 30-g PTTs (1.5–2.3% of the birds' body masses) on Terschelling. The males were selected to represent the total span of body masses within the catch. Males were chosen to avoid the potentially negative influence of the transmitter on the breeding performance of females (cf. Ward & Flint 1995). The birds were also marked with combinations of colour rings enabling individual recognition in the field after release.

The PTTs were glued to the back feathers of the birds just behind their shoulders with Loctite Superattak glue. The feathers at the attachment site were clipped halfway to their base before gluing, so that after attachment the PTTs would be partly covered by the surrounding feathers. In addition the PTTs were fastened with a harness made of soft elastic (2 g) as described by Glahder *et al*. (1996). The harness consisted of two loops around the body, both behind the wings. The harness was sealed with Loctite Superattak glue.

All the PTTs were programmed with a continuous transmission cycle of 10 h ON and 13 h OFF, running until battery exhaustion. With an expected battery life of about 600 h this would give relatively detailed information for the complete spring migration. In reality, battery life-times were much longer than anticipated in most cases, allowing us to follow several birds not only during spring migration but also throughout the whole summer and in some cases also during the first stages of autumn migration. However, here we present data only from the spring migration period to, and including, the birds' arrival at Taymyr.

The transmitters were followed via CLS/Service Argos in Toulouse, France. Depending on satellite orbits, bird behaviour, local conditions and possibly transmitter quality we received between one and 25 positions per day during spring migration. Generally the 30-g PTTs gave many more, and more accurate, positions than the 22-g PTT. Locations given by the Argos system are divided into different classes depending on validation, numbers of messages received and accuracy. In our analysis of stopover areas we have used only high-class positions (location class 1–3) with an estimated accuracy of less than 1 km. Positions of unspecified accuracy (0, A, B) were used to analyse departure and arrival times from these areas. Positions during flight were rarely within any of the higher accuracy classes. Thus we have, with a few exceptions (see below), used all available validated positions during flights to describe flight paths. In some cases, positions were discarded after visual inspection because flight speeds were unrealistically high and inconsistent with the distance from one position to another. An accuracy check of positions when the birds were still stationary at the catching sites revealed that the majority (75 and 68%) of positions of class 0 and A was within 20 km from the catching sites, i.e. within the area the birds were likely to use. For class B positions the corresponding figure was 32%. Bearing this degree of uncertainty in mind we only used class B positions when they indicated reasonable flight speeds between successive locations. It seems sound to use such positions only for descriptions of migratory movements over longer distances and time intervals as the results will only be affected to a small degree in such cases. The nine transmitters gave a total of 2741 validated positions during the spring migration periods. Of these 880 were used in the analysis.

Location times in UTC were used for all calculations of time intervals between positions. Distances and directions were based on standard calculations for loxodromes (rhumb-lines). When calculating migratory distances covered by the birds we used the distance between mean coordinates of high-class (1–3) positions for stopovers. To get a more detailed description of

the actual flight routes we also used one position taken each hour during bouts of migratory flight. In this way we eliminate errors made by inaccuracies in positions, and calculated distances are thus minimum distances travelled by the birds. As a basis for evaluating the flight routes and stopover areas the *Times Atlas of the World (Comprehensive Edition)* was used.

Periods of active flight were defined as periods when flight speeds exceeded 20 km/h (6 m/s) for successive positions. A flight episode (flight) was characterized as a period of uninterrupted flight between stops. Total flight time was calculated using the distance travelled by the birds and an assumed average flight speed (ground speed) of 70 km/h (19 m/s) (Green & Alerstam 2000) as exact departure/arrival positions were not given for all flights, thus not allowing us to calculate exact flight times. Stops were defined as periods with flight speeds of less than 20 km/h (6 m/s), lasting at least 1 h. In our analysis we have divided the stops into long-time and short-time stopovers. Stops exceeding 48 h were classified as long-time stopovers and those lasting less than 48 h as short-time stops. The basis for this division is that we find it more likely that stops exceeding 48 h are foraging stopovers with the possibility of net energy gain for the birds, whereas this is quite unlikely for birds staying less than 48 h. Exact times for stops were sometimes available as both arrival and departure positions were given, or positions close in time to arrival/departure so that these times could be calculated with an accuracy of 1 h. These data were used to calculate the average duration of short stops. For calculations of total stopover times however, these were rounded up to half days as exact stopover times were not available for all stops. Premigratory fattening time was calculated assuming a start of spring fattening at 15 April (Ebbinge & Spaans 1995).

Observational data on migration of Brent from Sweden and Finland were collected from voluntary field observers, and from Scania also from the regional report committee of the Swedish Ornithological Society (see Green 1998 for details). Field observations have earlier confirmed that the vast majority of all Dark-bellied Brent Geese migrate over these parts of Sweden and through the Gulf of Finland during spring (Leivo *et al.* 1994, 1995, Green 1998). Wind data were collected from the European Meteorological Bulletin (EMB, Deutches Wetterdienst). Ground-level wind data (direction and speed) were used from one station in the Wadden Sea, one station in the Baltic Sea and three stations along the coast of the Arctic Ocean twice (00:00 and 12:00 UTC) each day for relevant periods in 1999. For each wind measurement occasion the wind effect (calculated groundspeed minus assumed airspeed, i.e. the wind assistance or resistance that the flying bird would get: positive in tailwinds and negative in headwinds) was calculated according to the method described by Piersma and Jukema (1990) and Piersma and van de Sant (1992). In the calculations it was assumed that Brent fly with an airspeed of 65 km/h (18 m/s) which is a reasonable approximation for the whole journey although in reality airspeeds are expected to vary due to several factors (Green & Alerstam 2000). Furthermore, migratory track directions coinciding with the average observed directions according to this study were used for each locality in the calculations.

RESULTS

Of the nine birds fitted with satellite transmitters eight were successfully tracked during the first stage of spring migration from the Wadden Sea to the White Sea. The lightest male in the 1999 catch did not migrate at all, but stayed in the Wadden Sea to moult. This bird was also observed at several locations in the Dutch Wadden Sea during the summer. It is excluded from further analysis.

Of the remaining eight birds, one transmitter failed shortly after arrival in the White Sea (bird F, Table 1). Six adult males in 1999 were successfully tracked all the way to Taymyr (birds A–E, G, Table 1) and the juvenile female in 1998 was tracked to northern Yamal peninsula (bird H, Table 1).

Field observations, departure of transmitter birds, general timing and winds during migration

Spring migration of Brent through the Baltic in 1998 was most intense between 18 and 31 May when a total of 35 000 birds were observed in Scania, the southernmost province of Sweden. Marked peak days were 18–19 May, 23–24 May and 31 May. Smaller numbers were seen in early June and the last migrating birds of the season were observed on 18 June. Bird H, a juvenile female, left Schiermonnikoog for the mainland coast in late May but stayed in the Netherlands at least until 2 June. She left the Netherlands sometime between the evening of 2 June and the next morning, as positions were received from Germany in the afternoon of 3 June.

In 1999, after a favourable change in wind direction (Fig. 1), mass departure from Terschelling was

Table 1. Summary statistics of the spring migration for eight Dark-bellied Brent Geese 1998–1999, as recorded by satellite telemetry. Overall migration speed was calculated from departure from the Wadden Sea. Migration speed shown within parentheses was calculated with the fat deposition period at the Wadden Sea included, assuming a start of fat deposition at 15 April.

Bird ID	Start date	End date	Total distance (km)	No. of flights	No. of stopovers > 48 h	No. of stopovers < 48 h	Overall migration speed (km/day)
A	19–20 May	27 June	5090	16	6	9	134 (70)
B	20 May	6 July	4577	14	4	9	97 (57)
C	20–21 May	8 July	5044	16	6	9	105 (61)
D	25–26 May	8 July	4968	12	6	5	116 (60)
E	20–21 May	9 July	5186	22	5	16	106 (62)
F[a]	20 May		2200	3	1	2	
G	3 June	8 July	5164	19	3	15	148 (62)
H (juv)[b]	2–3 June	8 July	4139	11	4	6	115 (49)
Average, Adults[c]			5004	16.5	5.0	10.5	118 (62)

[a]Transmitter failure, stopped after 15 days, incomplete migration.
[b]Data from 1998.
[c]Bird A–E and G, excl. birds F and H.

observed in the evening of 20 May, followed by mass migration over Scania the next day. Flocks were observed over south Sweden for most of the day but migration was particularly intensive during the evening when about 50 000 Brent passed Lund, Scania, in 3 h. In south Finland more than 100 000 birds were observed during 22–23 May, most of them on 22 May. Lower numbers were then seen passing south Sweden until around mid-June with the last significant numbers (about 5000 birds) on 5 June. The first transmitter-carrying bird left the Netherlands sometime between 19 May 21:00 h and 20 May 11:00 h. Four more birds left within the main exodus, between the evening of 20 May and the next morning. All five gave positions as they passed south Sweden within the heavy migration wave on 21 May, and south Finland during 22–23 May. The next bird to leave the Wadden Sea departed between 25 May 15:00 h and 26 May 02:00 h. The last bird departed on 3 June. This bird had left Terschelling on 13 May to continue spring staging on the nearby island of Ameland. All other birds stayed at Terschelling until departure from the Netherlands.

None of the birds migrated to their summer destinations in a single flight, but made several stopovers, lasting between a few hours and 17 days. Arrival on the breeding or moulting grounds did not take place until between late June and early July. The bird in 1998 (H) arrived at Bely Island, north of Yamal peninsula, on 8 July. As the transmitter failed on the next day, we cannot exclude the possibility that she did in fact continue further east after this date. The first bird to arrive at Taymyr in 1999 (A) did so on 20 June. He continued to move around for another 7 days and reached his final destination on 27 June. Here he spent the summer. The remaining five birds (B–E, G) reached Taymyr between 3 and 7 July. Three of them moved around for a couple of days after this and reached the summering localities between 6 and 9 July.

Favourable (tail) winds dominated during late May and early June in 1999 along the passage from the Wadden Sea to the White Sea (Fig. 1a,b). During this passage all birds selected migration days with wind assistance (Fig. 1a,b). Winds along the coasts of the Arctic Ocean in June and early July were more variable but good winds also occurred for the geese during this stage (Fig. 1c–e). Once again the birds moved on days with supporting winds (Fig. 1c–e). A more detailed analysis of migratory behaviours in relation to wind will be presented elsewhere.

Migration routes

The migration tracks of the eight birds that left the Wadden Sea are shown in Fig. 2. The figure shows the complete tracks, i.e. including movements within Taymyr peninsula in late June–early July, or until the transmitter failed. It is worth mentioning that although the routes taken by the different birds are very similar, none of them migrated with any other satellite-tagged bird.

Figure 3 compares the migration tracks with the great circle and constant geographical bearing routes between the Wadden Sea and Taymyr. The great circle (orthodrome) is the shortest path between two points

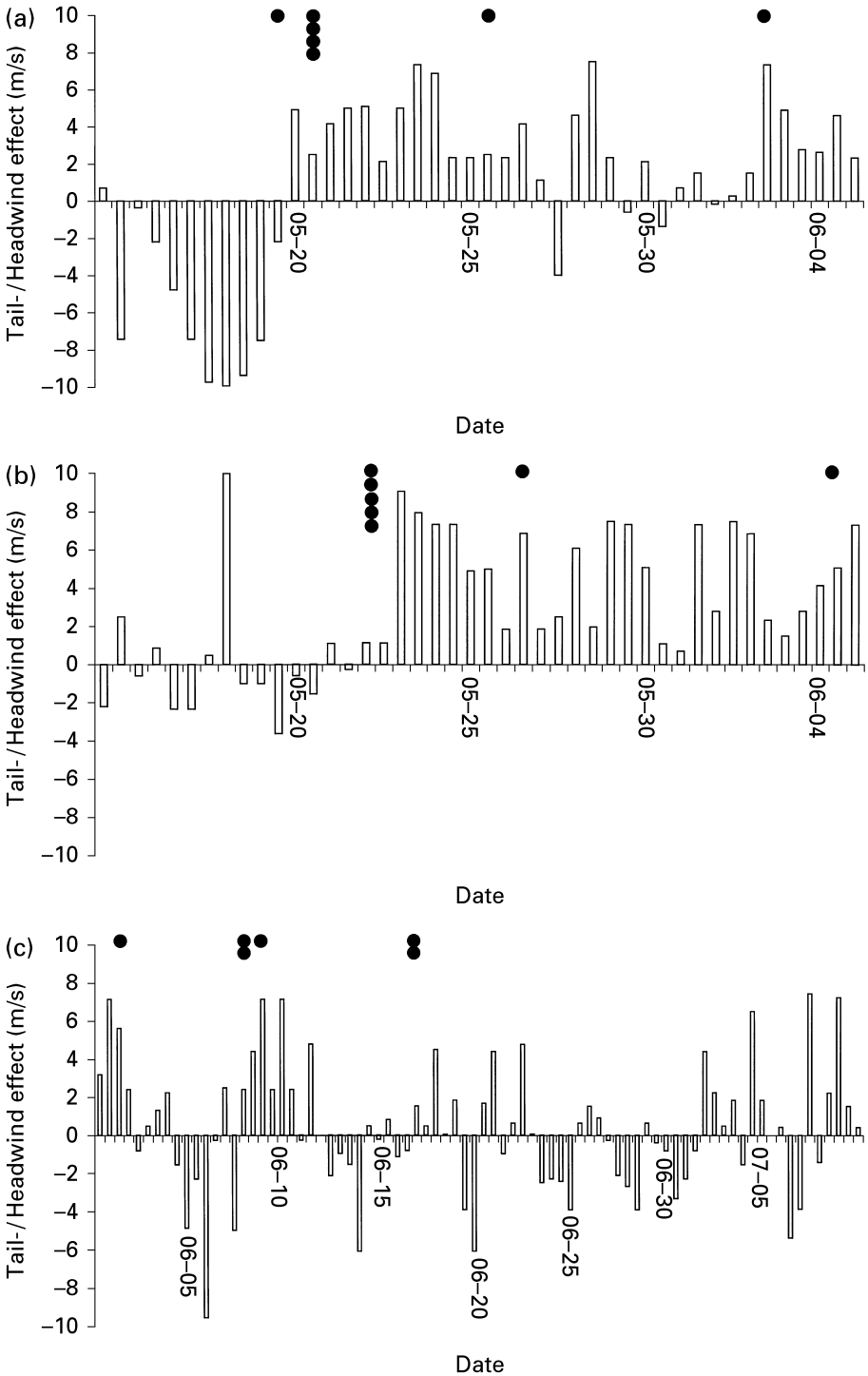

Figure 1. Tailwind (positive) and headwind (negative) effects (calculated groundspeed along mean migratory direction minus airspeed) for satellite-tracked Brent Geese at (a) Wadden Sea, (b) Baltic Sea, (c) Kanin peninsula, (d) Vaygach Island and (e) Yavay peninsula during spring 1999. In a and b the period 15 May–5 June is shown; c–e show the period 1 June–10 July. Dots above bars show when the different individuals passed the respective locality. Note that a–d are based on two wind measurements per day while e is based on only one wind measurement per day.

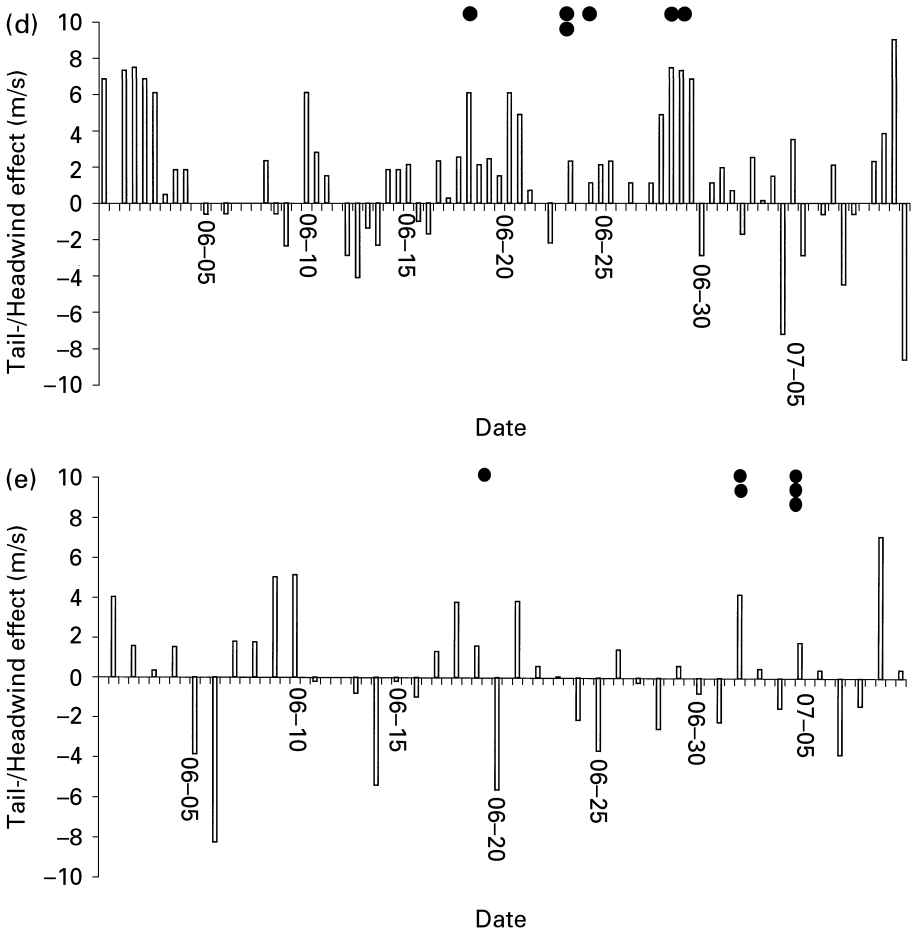

Figure 1. *Continued.*

on the Earth's surface. Depicted on a Mercator projection as here it will appear as a curved arc, while a constant geographical course (loxodrome, rhumb-line) will appear as a straight line. The great circle distance between the Wadden Sea and the final summer destinations of the birds is about 4300 km and the loxodrome is about 4700 km, making a flight along a great circle about 400 km shorter. However, the average flight distance calculated from the transmitter positions was 5000 km for the birds followed all the way to Taymyr (Table 1). Thus the birds were actually travelling at least 700 km (16%) further than the shortest possible route to their destinations.

Flights

On average the birds made 16 flights to reach their summer destinations on Taymyr, with varying periods of stopover in between (Fig. 2, Tables 1 and 2). The adult birds, tracked all the way to Taymyr (A–E, G), used significantly fewer flights to cover the first half of the migration, from the Wadden Sea to the Kanin peninsula, than to cover the second half from Kanin to Taymyr (Table 2, paired *t*-test: $t = -5.00$, $df = 5$, $P = 0.004$). As a result, the average flight distance between stops was longer for the first half than for the second (Table 2, paired *t*-test: $t = 5.65$, $df = 5$, $P = 0.002$). Although flights were generally shorter during the latter stage of migration, they did not become successively shorter as the birds approached their destinations. All birds made some longer flights (400–700 km) towards the end of migration, mainly between the Yamal and Taymyr peninsulas (Fig. 2). The longest flights during the second stage of migration were, however, shorter than the longest flights during the first part (Table 2, paired *t*-test: $t = 7.87$, $df = 5$, $P = 0.001$). The juvenile bird H in 1998 showed the same general pattern as the adults, with longer flight steps on average over the first stage than the second (Table 2).

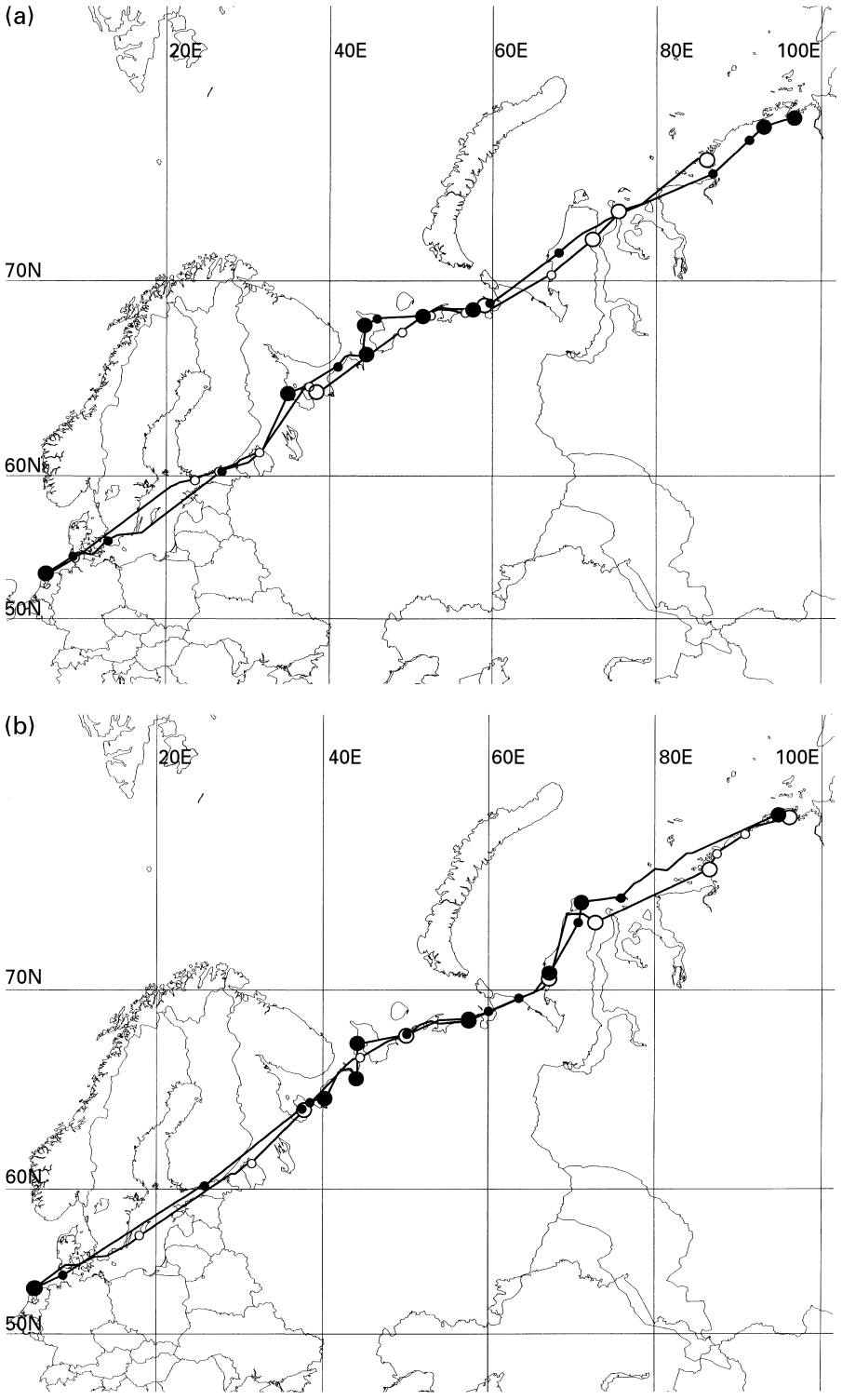

Figure 2. Spring migration tracks of eight Dark-bellied Brent Geese during 1998 (bird H) and 1999 (birds A–F). Large symbols show long-time stopovers (> 48 h), small symbols show short stops (< 48 h). (a) Filled circles, bird A; open circles, bird B. (b) Filled circles, bird C; open circles, bird D. (c) Filled circles, bird E; open circles, bird F. (d) Filled circles, bird G; open circles, bird H. The maps are in the Mercator projection.

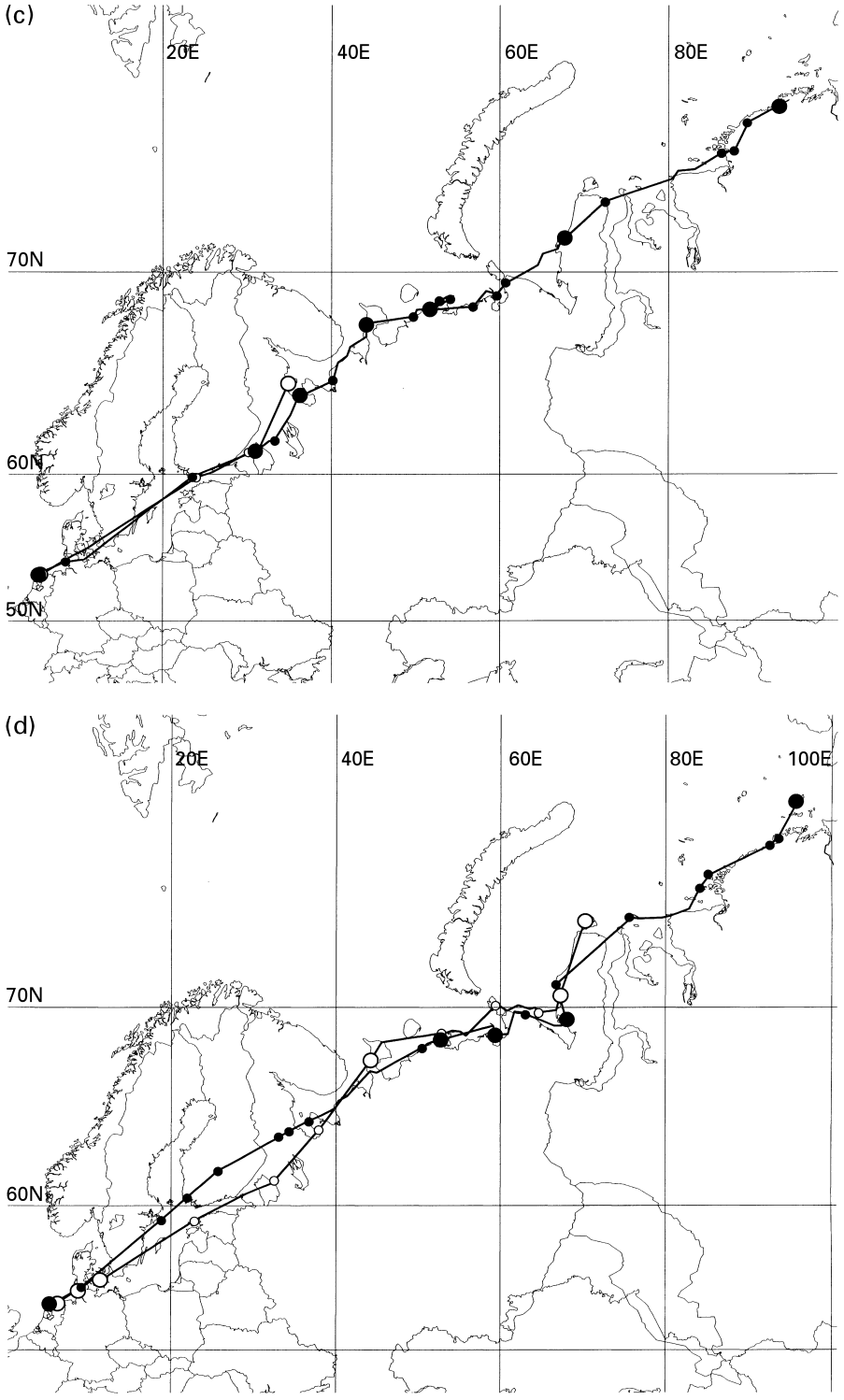

Figure 2. *Continued.*

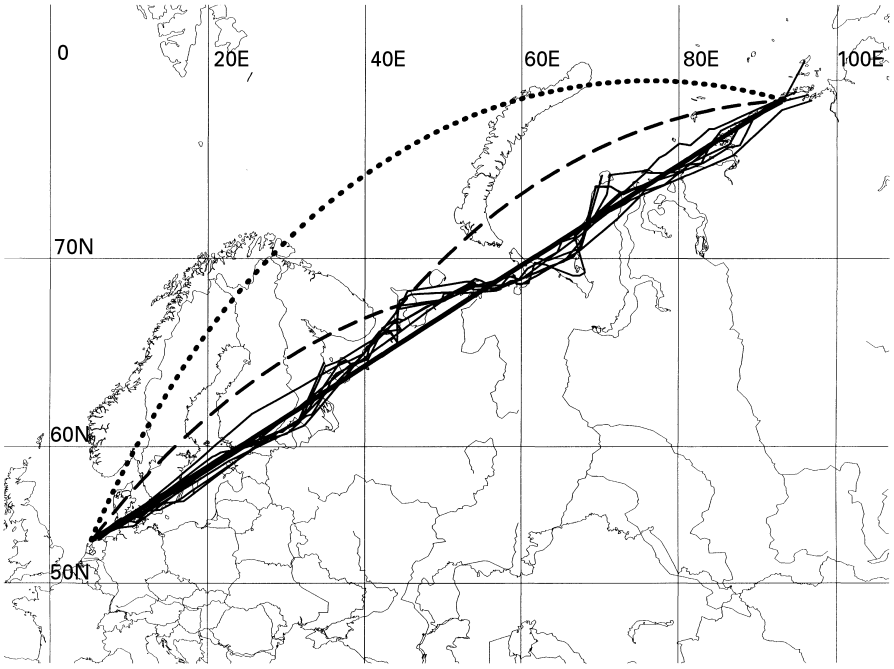

Figure 3. Spring migration tracks of eight Dark-bellied Brent Geese during 1998 and 1999 (thin lines) in comparison with the great circle (orthodrome, dotted curved arc) and the constant geographical course (loxodrome, straight bold line) between the Wadden Sea and Taymyr. Also shown is a great circle route with one stopover at Kanin peninsula (broken curved arcs). The map is in the Mercator projection.

Table 2. Data on number of flights and flight length between stops (both short and long stops, see text) for eight Dark-bellied Brent Geese for the first and second half (Wadden Sea – Kanin peninsula and Kanin peninsula – Taymyr peninsula) during spring migration 1998–1999.

	Wadden Sea–Kanin			Kanin–Taymyr		
Bird ID	No. of flights	Mean flight length (km)	Longest flight (km)	No. of flights	Mean flight length (km)	Longest flight (km)
A	6	466	989	10	229	732
B	6	396	1059	8	275	578
C	6	455	1220	10	232	633
D	4	679	923	8	282	476
E	7	404	1115	15	160	485
F[a]	3	733	1331	–	–	–
G	8	362	768	11	223	428
H[b]	6	449	810	5	289	406
Average Adults[c]	6.2	460	1056	10.3	234	555

[a]Transmitter failure, stopped after 15 days, incomplete migration.
[b]Data from 1998, juvenile bird.
[c]Excluding birds F and H, except for calculation of average longest flight where F is included.

Stopovers

Stopover localities used by the birds, and stopover durations, are shown in Fig. 2, Fig. 4 and Table 3. Although there were large individual differences in the use of different stopover localities, some general patterns were common to the majority of the birds. Generally, prolonged stops were made in the White

Figure 4. Map over the Russian arctic coast between the White Sea and Taymyr peninsula showing stopover localities used by eight Dark-bellied Brent Geese during spring migration in 1998 and 1999.

Sea – Kanin area, in three areas between the Kanin and Yugorskij peninsulas and at the Yamal peninsula. All birds made several short stops between the Wadden Sea and the White Sea (Fig. 2, Table 3). At least six birds made stops (mainly short stops) in Schleswig-Holstein. It is possible that the remaining two birds behaved in the same way but as the transmitters were in the 13-h-off phase during their departure from the Netherlands and passage through Schleswig-Holstein, we could not analyse this in detail. Six birds stopped (short stops) in the Gulf of Finland and at least four birds made short stops at Lake Ladoga. Bird E made a longer stop at the same locality (Table 3). Inland stops were rare apart from the ones at Lake Ladoga. Bird E, however, made an additional short inland stop at a lake between Lake Ladoga and Lake Onega (Fig. 2). Bird G made an inland stop at Lake Päijänne, central Finland, and two more inland stops at smaller lakes south-west of the White Sea (all short stops; Fig. 2). The short stops between the Netherlands and the White Sea lasted on average for 9.5 h (range 1–18 h, sd ± 6.2 h, n = 19 stops made by eight birds) with no apparent differences between sites.

The localities chosen for short stops during the second stage of migration often coincided with localities where other individuals made longer stops (Fig. 2, Table 3). Short stops during the second stage of migration were on average slightly longer (13.2 h, range 1–24 h, sd ± 9.8 h, n = 10 stops made by four birds) than during the first half but not significantly so (t-test, ns).

Speed of migration and time budgets

Although recorded speeds during flight ranged between 58 and 109 km/h (16–30 m/s), it took the adults between 60 and 96 h (mean 72 h) to cover the distance (*c.* 2300 km) from the Wadden Sea to the White Sea (here we have excluded bird E that stopped in Lake Ladoga). The juvenile bird H spent about 180 h to cover the same distance. Hence, the strategy with alternating periods of flight and short stops resulted in an overall average travelling speed of 32 km/h (763 km/day) from the Wadden Sea to the White Sea. The latter stage of migration was conducted even more slowly due to the many stops. From the Kanin peninsula, it took the birds 10–26 days to reach Taymyr, giving an average travelling speed of 4 km/h (105 km/day). Bird H in 1998 showed a similar pattern, averaging 300 km/day for

Table 3. Stopover duration (days) at different sites for eight Dark-bellied Brent Geese during spring migration 1998–1999. s = short stops (< 48 h).

Bird ID	Schleswig-Holstein	Zeeland Öresund	Gulf of Finland	Lake Ladoga	Onega Bay, White Sea	Dvina Bay, White Sea	Mezen Bay, SW Kanin	West Kanin peninsula	Sengeyskiy Island–Kolokolkova Bay	Pesyakov Island–Khaypudyrskaya Bay	West Yamal peninsula	Bely Island	NE Yamal peninsula	Yeyav peninsula–Vilkitskogo Island	Taymyr peninsula
A	s		s		2		7	7	5	4	s				4
B	s	s	s	s		17			s	13	s		3	6	
C	s		s		s	2	7	16	s	5	4	8	s	s	
D				s	4			s	7	14	5		4		3
E	s		s	8	8	s		8	7	s	5		s		
F[a]			s	s	2										
G	s				s				7	12	2			s	
H	2	3	s	s	s			15		s	9	2[b]			

[a]Transmitter failure, stopped after 15 days, incomplete migration.
[b]The transmitter stopped giving signals after 2 days here, true stopover time not known. Not included in total stopover-time.

the first stage of migration compared with 131 km/day for the second stage. The overall speed of migration from the Wadden Sea to the summering grounds ranged between 97 and 148 km/day (Table 1). Including the premigratory fattening period in the Wadden Sea gave a total migration speed of 49–70 km/day (Table 1).

The flight distance between the Wadden Sea and Taymyr is equivalent to about 3 days and nights (72 h) of flight, assuming a mean groundspeed of 70 km/h (19 m/s) (Green & Alerstam 2000). As it took the birds on average 42 days to cover this distance, only 7% of the time during spring migration consisted of active flying. Long-time (foraging) stopovers made up the largest part (79%) of the total migration time, while 14% was spent at short-time stops (Table 4). Including the premigratory fuel deposition time in the Wadden Sea would lower the fraction of time spent in active flight to 4% and increase the time spent at foraging stops to 89%.

DISCUSSION

Delayed arrival at the breeding grounds – an effect of the transmitters?

It is always questionable whether a flying animal carrying a transmitter behaves normally. Although we aim to minimize any effect, it would probably be unrealistic to expect no effect at all. All our birds started migration within the normal departure period (cf. Ebbinge & Spaans 1995, Green 1998). Migration routes used by the transmitter-carrying birds were completely normal when compared to field data on mass migrations during recent decades (Saurola 1976, Green 1998, Syroechkovski & Litvin 1998). The timing of the first stage of migration corresponded well with observed patterns of migration in 1999, shown by the fact that several transmitter-birds passed over south Sweden and Finland during mass migration. Departure from the White Sea – Kanin area was also within normal time limits for several birds although some stayed beyond the normal departure dates for this area. Mass migration over the Kanin peninsula has been observed between 10 and 12 June (Kistchinski & Vronski 1979, Syroechkovski & Litvin 1998) and our birds left this area on 2 June, 9 June (two birds), 10 June, 17 June (two birds) and 27 June. The last stage of migration was, however, conducted much more slowly than expected. Comparing dates of mass departure from Kanin with mass arrival at the breeding

Table 4. Time budgets of the spring migration of eight Dark-bellied Brent Geese during spring migration as recorded by satellite telemetry 1998–1999. Calculations of flight-times are based on an assumed average groundspeed of 70 km/h. Time budget for a breeding bird is based on a departure from the Wadden Sea on 25 May and an arrival to Taymyr on 14 June.

Bird ID	Total flight time (h)	Total flight time (days)	Total time at long stops (days)	Total time at short stops (days)	Total time from departure to arrival (days)	Premigratory fattening time (days) assuming start at 15 April	Total time (days)
A	73	3	29	6	38	33	71
B	65	3	39	5	47	34	81
C	72	3	42	4	49	34	83
D	71	3	37	3	43	40	83
E	74	3	36	11	50	34	84
G	74	3	21	11	35	48	83
H	59	2.5	29	3.5	35	48	83
'Breeding bird'	70	3	12	6	21	39	60
Average of observed	70	3	33	6	42	39	81

grounds suggests that this stage of the migration is normally conducted without longer stops (Spaans *et al.* 1998, Syroechkovski & Litvin 1998). From 1990 to 1995 mass arrival at west Taymyr occurred between 10 and 20 June; our birds reached Taymyr between 20 June and 7 July. Nevertheless, arrival at Taymyr in late June and early July is typical of some birds (Frodin *et al.* 1994, T. Alerstam pers. obs., during the Swedish–Russian Tundra expedition in 1994). Late-arriving birds are probably non-breeders (including immature birds). As incubation and brood-rearing takes about 70 days (Cramp & Simmons 1977), birds arriving in late June and early July will simply not have time to breed successfully in the short Arctic summer. We conclude that the transmitter-birds behaved normally during the first stage of spring migration, with regards to both timing and routes. For some reason they decided not to make a breeding attempt and thus conducted the second stage more slowly than normal (for breeding birds), although the routes used during this stage were also normal. The behaviour of the juvenile bird in 1998 might have been completely normal for a young bird. Juveniles leave the Wadden Sea later than adults (Spaans 1987), and it seems plausible that they migrate more slowly than adults as they do not face the time constraints of breeding (Bergmann *et al.* 1994).

Clearly, carrying the transmitters did not prevent the birds from reaching the breeding areas. As several birds also conducted a successful autumn migration, carrying a transmitter does not seem to impair migratory performance seriously. Why then did our birds forego breeding and prolong the second half of their migration? We can only speculate about this, but as 1999 generally was a good breeding year (23.5% juveniles among wintering birds in the UK, R. Hearn pers. comm., about 25% juveniles in the Netherlands, K. Koffijberg pers. comm.) it is unlikely that the birds encountered signs of high predation pressure along the route (cf. Spaans *et al.* 1998). The birds were probably not held back by unfavourable winds during migration either. Migration is usually delayed in years when headwinds prevail (Ebbinge 1989, Green 1998) although the geese will eventually migrate if no change occurs despite the unfavourable situation. Breeding results in such years are usually poor as the birds probably use too much of their nutrient reserves during the flight (Ebbinge 1989).

Winds during the flight from the Wadden Sea to the White Sea were generally good in 1999 (Fig. 1), and even during the latter stage of migration there were occasions when winds were favourable before most of the geese eventually made the final flights towards their summer destinations (Fig. 1). Furthermore the geese actively selected migration days when tailwinds occurred. Thus it is unlikely that the failure to breed was caused by migration conditions. We also find it unlikely that carrying the transmitter and/or the harness affected foraging or energy uptake so that the birds could not put on enough fat and protein for long-distance flights. Five of the birds were observed at Terschelling between their capture and migration, and foraging behaviour seemed completely normal in all cases. It is possible that carrying a transmitter might break pair-bonds, and that unpaired males migrate more slowly than paired ones. We do have some data on the pair status of our males at catching; the lightest male was single and at least four others were paired. As most adult birds are paired during spring (Ebbinge & Spaans 1995) we

assume that the other three were paired too. Of the four birds resighted at Terschelling in autumn 1999 three were paired, and one was of unknown status, which does not support this explanation. Interestingly, the partner of bird F returned with an unmarked male and two offspring. The transmitter failure in the White Sea of bird F might indicate that the bird was killed. Despite this his partner apparently managed to find a new mate during spring migration. So, poor condition of female partners seems a very unlikely explanation for the slow migration observed. The most likely explanation therefore, although speculative, is that carrying the transmitters made the birds decide not to breed. As Brent can apparently make this decision before reaching the breeding areas (Spaans *et al.* 1998), adding a weight, although small, might make a Brent switch behaviour from intending to breed to just travelling more slowly to moulting areas. Ward and Flint (1995) fitted radio-transmitters, similar in size to our satellite transmitters, to Black-bellied Brent Geese *B. b. nigricans* in North America and reported that this might make them refrain from breeding. Although their birds reached the breeding grounds at the normal time, they did not breed.

Routes

The routes followed by the Brent were clearly closer to constant geographical courses than to great circle routes. The influence of coastlines was evident (Figs 2 and 3). Why do Brent follow a flight path to their breeding quarters that is about 16% longer than the shortest possible route? Following a great circle route requires special navigational skills as headings have to be adjusted continuously (Alerstam & Pettersson 1991). Several mechanisms for great circle orientation have been suggested and at least some waders, terns and skuas seem to follow orthodrome-like routes when migrating between Eastern Siberia and North America (Alerstam & Gudmundsson 1999).

Apart from the navigational difficulties, the possibilities for replenishing nutrient stores would clearly be limited along a great circle route from Western Europe to Siberia. The last feeding site would probably be west Denmark, after which the geese would have to fly all the way to Taymyr before finding the next opportunity (Fig. 3).

This simply might not be a viable option for the birds. It is cheaper, in terms of absolute fuel costs, to make shorter flights with smaller fuel loads than to fly the same distance in one long flight with a large fuel load (Alerstam 1979, Piersma 1987). To cover a flight distance of 4300 km in one step requires a fuel load (mass of fuel in relation to lean body mass) of about 0.6 for a Brent (cf. below). Dividing the journey into two equal steps with correspondingly smaller fuel loads leads to reduced total energy costs for the transport, even when the divided journey is a detour with up to 12–17% (depending on flight mechanical range equation) further than the direct route. If the journey is divided into further flight steps (with intervening fuel deposition) energy savings will increase yet again, making even longer detours advantageous (Alerstam 2001). Ebbinge and Spaans (1995) analysed flight costs for spring migrating Brent. They concluded that only geese starting with a body mass close to 2 kg (lean body mass 1.2–1.3 kg) could reach the breeding grounds in a direct flight with enough nutrient stores left to breed successfully. In their analysis, Ebbinge and Spaans did not consider differences between orthodromes and loxodromes but assumed that Brent flew along the 4300 km great circle route. Mean departure body masses in the Wadden Sea of Dark-bellied Brent are in the range of 1500–1700 g (Ebbinge & Spaans 1995) and thus most birds could not reach Taymyr in one flight and arrive in breeding condition. However, Brent of other populations do frequently depart with body masses approaching 2 kg (Gudmundsson *et al.* 1995, Clausen & Bustnes 1998). Birds flying along an orthodrome to Taymyr with a body mass of 2 kg would be near the limit of flight performance. Brent probably cannot carry fuel loads resulting in body masses over 2 kg (Hedenström & Alerstam 1992). Thus birds would be totally dependent on good flight conditions, having no reserves to deal with headwinds encountered en route. Such a flight would also be perilous as a large part of the route passes over the Arctic Ocean (Fig. 3).

For these reasons, flying along an orthodrome seems unlikely both for energetic and safety reasons. But why then not divide the migration into two orthodromes, one between the Wadden Sea and the White Sea/Kanin and one between Kanin and Taymyr? Flying approximately along a loxodrome between west Europe and Siberia let the Brent keep contact with the coast (Fig. 3). Some of the coastal areas allow the birds to forage and replenish their nutrient stores. Coastlines may also provide leading lines, visual reference marks for navigation, making it easier to follow the traditional routes that goslings learn during their first migration. Furthermore, coasts may offer sheltered places to sit out bad

weather if encountered, and offer fresh water if the birds need to drink.

Flight behaviour during the first stage of migration

The geese did not fly the first 2500 km of their migration from the Wadden Sea to the White Sea area in a single flight. Several short stops were made and mean flight length was 450–500 km corresponding to a flight duration of 6.5–7 h with an assumed groundspeed of 70 km/h (19 m/s) (Green & Alerstam 2000). The longest flights were on average 1000 km with maximum recorded lengths of 1300 km (Table 2). This means sustained flights of 14–19 h. The strategy of making short stops was apparently not only used by the transmitter-birds as the overall progress of the main migration wave over south Sweden and Finland followed the same timing as for our birds.

Light-bellied Brent Geese *B. b. hrota* have also been found to use short stops en route (Clausen & Bustnes 1998) resulting in overall migration speeds of 32–38 km/h (flight periods + stops combined) for the 2700–3500 km flights between Denmark and Svalbard or Greenland. Overall migration speeds for the birds in this study during the Wadden Sea – White Sea stage were 33–38 km/h. The same pattern of mixing flights with short stops was also found for Barnacle Geese *Branta leucopsis* during autumn migration from Svalbard to Scotland (Butler *et al.* 1998). The longest flights performed by the Barnacle Geese were of similar length to the longest flights found in this study.

There seems to be a general pattern that larger waterfowl do not fly more than about 1500 km without taking short stops. What is the reason for this? Short stops were not principally for food. Of the stopover sites in this study only the Schleswig-Holstein coast provides suitable feeding areas for Brent, and in the Baltic, stops were made at sites where the birds had little opportunity to feed. Stops may be taken because the birds need to drink. Brent have quite large salt glands (Bergmann *et al.* 1994) and may be able to utilize seawater. When Brent feed on *Zostera* offshore in Denmark they never go to freshwater to drink, but drink seawater (P. Clausen pers. obs.). Satellite tracking data from Whooper Swans *Cygnus cygnus* flying between Iceland and Scotland indicated that the birds made short stops during inclement weather and/or complete darkness. This suggested that stops were made when the birds lost their visual orientation cues (Pennycuick *et al.* 1999). This seems unlikely for Brent migrating when and where there is little darkness. Furthermore, weather conditions were excellent for the whole migration period in 1999. Although speculative, the most likely explanation is that the birds stop to drink or rest.

Short stops during the second stage of the migration were often taken at sites where other birds made longer stops and it is possible that, in addition to the above-mentioned factors, some of the stops were made to scout for potential long-stop sites. Stops made at the Yamal and Taymyr peninsulas may also have been made in search of suitable breeding or moulting sites.

Speed of migration

The overall speeds of migration found in this study agreed with predictions made from flight mechanical theory. Alerstam (2000) predicted that Brent would achieve overall migration speeds (including stopovers and flight time) of between 40 and 75 km/day, for the range of fuel deposition rates found during spring staging of about 12 g/day, equivalent to 0.5–1 times Basal Metabolic Rate (Ebbinge & Spaans 1995). Our birds achieved overall migration speeds in the range of 49–70 km/day, including an assumed fuel deposition period starting at 15 April in the Wadden Sea (Ebbinge & Spaans 1995). As our birds arrived late at the breeding grounds, we assume that the overall migration speed of a Brent Goose arriving in normal time for breeding would be a little bit higher, about 85 km/day, but still near to the predicted range. The overall migration speeds of Brent were much lower than those found for birds using both flapping and soaring flight, like raptors and storks, which frequently reach overall speeds of 150–250 km/day (Berthold *et al.* 1995, Meyburg *et al.* 1995, Kjellén *et al.* 2001). The percentage of time spent in active migration (flight) was also low in our birds compared to soaring flyers. While the Brent on average spent 7% of the total migration time in active flight, the corresponding percentage for Ospreys *Pandion haliaetus*, satellite tracked during autumn migration between Sweden and Africa, was between 15 and 38% (the original figures from Kjellén *et al.* 2001 of 40 and 100% corrected for the fact that Ospreys only migrate for about 9 h per day). Also a calculated active flight percentage for a Brent Goose arriving at Taymyr at the normal breeding time (14%) would be lower than that found for the Ospreys. This supports the theoretical prediction that soaring flight (or a combination of soaring and flapping flight) gives

higher migration speeds than flapping flight for larger bird species (Hedenström 1993, Hedenström & Alerstam 1998).

The reason for the slow migration speed of Brent and other large waterfowl (see Hedenström & Alerstam 1998) is their low fuel deposition rates in combination with a relatively high flight power. Increasing fuel deposition rates to 1.5–2 times BMR instead would theoretically increase overall migration speeds to 120–150 km/day (Alerstam 2000). However, as Brent Geese are herbivores, they are physiologically constrained by the low digestibility and nutrient value of their food, and are probably achieving fuel deposition rates close to the maximum possible (Prop & Deerenberg 1991). Thus these birds are attaining migration speeds close to what is possible for them.

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REFERENCES

Alerstam, T. 1979. Wind as a selective agent in bird migration. *Ornis Scand.* **10**: 76–93.

Alerstam, T. 2000. Bird migration performance on the basis of flight mechanics and trigonometry. In Domenici, P. & Blake, R.W. (eds) *Biomechanics in Animal Behaviour*: 105–123. Oxford: BIOS Scientific Publishers Ltd.

Alerstam, T. 2001. Detours in bird migration. *J. Theor. Biol.* **209**: 319–331.

Alerstam, T. & Gudmundsson, G.A.G. 1999. Migration patterns of tundra birds: tracking radar observations along the Northeast Passage. *Arctic* **52**: 346–371.

Alerstam, T. & Pettersson, S.-G. 1991. Orientation along great circles by migrating birds using a sun compass. *J. Theor. Biol.* **152**: 191–202.

Beekman, J.H., Berthold, P., Nowak, E. & Querner, U. 1996. Implementation of satellite tracking in studying migration of Anatidae: an overview and a case study. *Gibier Faune Sauvage* **13**: 157–176.

Bergmann, H.-H., Stock, M. & ten Thoren, B. 1994. *Ringelgänse*. Wiesbaden: AULA-Verlag.

Berthold, P., Nowak, E. & Querner, U. 1995. Satellite-Telemetrie eines Zugvogels von Mitteleuropa bis in das südafrikanische Winterquartier: eine Fallstudie am Weisstorch (*Ciconia ciconia*). *J. Ornithol.* **136**: 73–76.

Butler, P.J., Woakes, A.J. & Bishop, C.M. 1998. Behaviour and physiology of Svalbard Barnacle Geese *Branta leucopsis* during their autumn migration. *J. Avian Biol.* **29**: 536–545.

Clausen, P. & Bustnes, J.O. 1998. Flyways of North Atlantic Light-bellied Brent Geese *Branta bernicla hrota* reassessed by satellite telemetry. In Mehlum, F., Black, J. & Madsen, J. (eds) *Research on Arctic Geese. Proceedings of the Svalbard Goose Symposium, Oslo, Norway*: 23–26 September 1997. *Norsk Polarinstitutt Skrifter* **200**: 227–242.

Cramp, S. & Simmons, K.E.L., eds. 1977. *Birds of the Western Palearctic*, Vol. 1. Oxford: Oxford University Press.

Ebbinge, B.S. 1989. A multifactorial explanation for variation in breeding performance of Brent Geese *Branta bernicla. Ibis* **131**: 196–204.

Ebbinge, B.S. & Spaans, B. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent Geese *Branta b. bernicla* in the high Arctic. *J. Avian Biol.* **26**: 105–113.

Frodin, P., Haas, F. & Lindström, Å. 1994. *Bird migration at Sibiryakov Island, Taymyr, Siberia in early summer 1992*. Lund: Department of Ecology, Lund University.

Fuller, M.R., Seegar, W.S. & Howey, P.W. 1995. The use of satellite systems for the study of bird migration. *Israel J. Zool.* **41**: 243–252.

Glahder, C., Fox, A.D. & Walsh, A.J. 1996. Effects of fitting dummy satellite transmitters to Greenland White-fronted Geese *Anser albifrons flavirostris. Wildfowl* **48**: 88–97.

Green, M. 1998. Spring migration of Barnacle Goose *Branta leucopsis* and Dark-bellied Brent Goose *Branta bernicla bernicla* over Sweden. *Ornis Svecica* **8**: 103–123.

Green, M. & Alerstam, T. 2000. Flight speeds and climb rates of Brent Geese: mass-dependent differences between spring and autumn migration. *J. Avian Biol.* **31**: 215–225.

Gudmundsson, G.A., Benvenuti, S., Alerstam, T., Papi, F., Lilliendahl, K. & Åkesson, S. 1995. Examining the limits of flight and orientation performance: satellite tracking of brent geese migrating across the Greenland ice-cap. *Proc. R. Soc. Lond. B* **261**: 73–79.

Hedenström, A. 1993. Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Phil. Trans. R. Soc. Lond. B* **342**: 352–361.

Hedenström, A. & Alerstam, T. 1992. Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. *J. Exp. Biol.* **164**: 19–38.

Hedenström, A. & Alerstam, T. 1998. How fast can birds migrate? *J. Avian Biol.* **29**: 424–432.

Kistchinski, A.A. & Vronski, N.V. 1979. Migrations of Brent Geese *Branta bernicla*. In Kistchinski, A.A. (ed.) *Migrations of Birds of Eastern Europe and Northern Asia, Ciconiiformes – Anseriformes*: 188–202. Moscow: Nauka (in Russian).

Kjellén, N., Hake, M. & Alerstam, T. 2001. Timing and speed of migration in male, female and juvenile Ospreys *Pandion haliaetus* between Sweden and Africa as revealed by field observations, radar and satellite tracking. *J. Avian Biol.* **32**: 57–67.

Leivo, M., Kontiokorpi, J. & Rusanen, P. 1994. [Migration of arctic waterfowl on the northern Baltic sea in spring 1993]. *Linnut* **29** (2): 12–19. (in Finnish with English summary).

Leivo, M., Kontiokorpi, J. & Rusanen, P. 1995. [Migration of arctic waterfowl on the northern Baltic sea in spring 1994]. *Linnut* **30** (3): 28–31. (in Finnish with English summary).

Meyburg, B.-U., Sheller, W. & Meyburg, C. 1995. Zug und Überwinterung des Schreiadlers *Aquila pomarina*: Satellitentelemetrische Untersuchungen. *J. Ornithol.* **136**: 401–422.

Pennycuick, C.J., Bradbury, T.A.M., Einarsson, Ó. & Owen, M. 1999. Response to weather and light conditions of migrating Whooper Swans *Cygnus cygnus* and flying height

profiles, observed with the Argos satellite system. *Ibis* **141**: 434–443.

Piersma, T. 1987. [Hop, skip or jump? Constraints on migration of arctic waders by feeding, fattening and flight speed]. *Limosa* **60**: 185–194 (in Dutch with English summary).

Piersma, T. & Jukema, J. 1990. Budgeting the flight of a long-distance migrant: Changes in nutrient levels of Bar-tailed Godwits at successive spring staging sites. *Ardea* **78**: 315–337.

Piersma, T. & van de Sant, S. 1992. Pattern and predictability of potential wind assistance for waders and geese migrating from West Africa and the Wadden Sea to Siberia. *Ornis Svecica* **2**: 55–66.

Prop, J. & Deerenberg, C. 1991. Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* **87**: 19–28.

Saurola, P. 1976. The role of the Finnish archipelago in the passage of northern sea- and shorebirds. In Kumari, E. (ed.) *Bird Migration*: 41–44. Talin: Valgus.

Spaans, B. 1987. Met de Texelse Rotganzen op reis. *De Levende Natuur* **88**: 194–199.

Spaans, B., Blijleven, H.J., Popov, I.U., Rykhlikova, M.E. & Ebbinge, B.S. 1998. Dark-bellied Brent Geese *Branta bernicla bernicla* forego breeding when Arctic Foxes *Alopex lagopus* are present during nest initiation. *Ardea* **86**: 11–20.

Syroechkovski, E.E. Jr & Litvin, K.E. 1998. [Migrations of Brent Geese (*Branta bernicla bernicla*) in Russia.]. *Casarca* **4**: 71–95 (in Russian with English summary).

Ward, D.H. & Flint, P.L. 1995. Effects of harness-attached transmitters on premigration and reproduction of Brant. *J. Wildl. Manage.* **59**: 39–46.

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