

Site use by dark-bellied brent geese *Branta bernicla bernicla* on the Russian tundra as recorded by satellite telemetry: implications for East Atlantic Flyway conservation

Martin Green, Thomas Alerstam, Preben Clausen, Rudi Drent & Barwolt S. Ebbinge

Green, M., Alerstam, T., Clausen, P., Drent, R. & Ebbinge, B.S. 2002: Site use by dark-bellied brent geese *Branta bernicla bernicla* on the Russian tundra as recorded by satellite telemetry: implications for East Atlantic Flyway conservation. - Wildl. Biol. 8: 229-239.

In 1999, seven dark-bellied brent geese *Branta bernicla bernicla* were followed during spring migration from western Europe to Arctic Russia using satellite telemetry. For six of the birds we were also able to monitor their summer stay at the Taymyr Peninsula, and for five birds part of their autumn migration was recorded. In this article, we report on site use during summer and spring/autumn migration. We also describe migration routes and evaluate general migratory performance during autumn migration. All birds spent the summer within areas covered by the Great Arctic Reserve on the Taymyr Peninsula. None of the birds returned to the wintering area with young, so the sites used during summer were most likely used primarily for moulting. The birds remained at the same sites the whole summer until the start of autumn migration, indicating that the build-up of fuel stores for migration took place at the moulting sites. Autumn migration was conducted in a similar way as spring migration regarding routes and general migratory performance. Site use showed both a relatively large variation between individuals and seasons, as well as some degree of site fidelity as all birds returned for a longer stay in autumn to at least one of the areas they had used for more than two days in spring. Thus the migration of brent geese along the Arctic Ocean cannot be considered as a simple migration system with just a few key sites along the route, but instead it is a complex system with several localities used in different ways by different individuals. Most of the areas used by the satellite-tagged birds were previously known stopover areas, but some of them had not been recognised as being of importance for brent geese before. Most of the stopover areas do not have any kind of formal legal protection. It is suggested that further research should be carried out in the areas identified in this study to evaluate their importance and role in the migratory journeys of dark-bellied brent geese.

Key words: Branta bernicla, conservation, migratory performance, Russian tundra, satellite telemetry, site use, waterfowl

Martin Green & Thomas Alerstam, Department of Animal Ecology, Ecology Building, S-223 62 Lund, Sweden - e-mail addresses: martin.green@zoekol.lu.se (Martin Green); thomas.alerstam@zoekol.lu.se (Thomas Alerstam) Preben Clausen, National Environmental Research Institute, Department of

Coastal Zone Ecology, Kalø, Grenåvej 12, DK 8410 Rønne, Denmark - e-mail: pc@dmu.dk

Rudi Drent, Zoological Laboratory, University of Groningen, Pb 14, 9750 AA Haren, Netherlands - e-mail: S.C.Bakker-Geluk@biol.rug.nl

Barwolt S. Ebbing, Alterra, Pb 47, NL-6700 AA Wageningen, The Netherlands - e-mail: B.S.Ebbing@alterra.wag-ur.nl

Corresponding author: Martin Green

Received 15 February 2001, accepted 9 October 2001

Associate Editor: Jesper Madsen

In spring 1999, we supplied eight dark-bellied brent geese with light-weight satellite transmitters during spring staging in the Dutch part of the Wadden Sea. The general aim of the project was to get detailed data on individual migration performance during spring migration. The results gathered concerning e.g. flight lengths, routes and timing during spring migration has been presented elsewhere (Green, Alerstam, Clausen, Drent & Ebbing 2002; R. Drent, P. Clausen, M. Poot, V. Andreev, M. Green & B.S. Ebbing, unpubl. data). Seven birds were tracked to the first major Arctic stopover area (the White Sea, northwest Russia) and six birds were followed all the way to presumed breeding or moulting grounds in north central Arctic Russia (Green et al. 2002). As it turned out, the transmitters functioned much longer than we anticipated, and we were able to follow the birds not only during spring migration but also during summer (six birds) and for a varying part of autumn migration (five birds). In this article, we present the results from the summer and autumn parts of the satellite trackings focusing on site use, as well as a comparison of behaviour during spring and autumn migration.

Studying individual migration performance and answering questions about how birds behave in detail during migration may seem purely academic, but that is a misjudgement. Safeguarding a population of a migratory species requires detailed knowledge about behaviour during migration and for instance maximum distances between necessary stopover sites, before one can decide on minimum requirements of a network of protected sites along a flyway, a necessary basis before well-justified flyway management plans really can be made (Davidson & Stroud 1996). Satellite telemetry can provide the data needed for making conservation plans of long-distance migratory birds, i.e. identifying important stopover areas, finding out what roles different stopover sites play in the annual cycle of a population and how these sites are used in relation to each other as well as answering questions about individual variation

in migration strategies within a population (Davidson & Stroud 1996, Haig, Mehlman & Oring 1998, Lorentsen, Jostein Öien & Aarvak 1998, Davidson, Bryant & Boere 1999). The method is especially well suited to study such questions in areas where the collection of field data using other methods is difficult, such as for instance high Arctic areas. Due to the high costs associated with the method it can be applied only to a few individuals of a population. However, the information gathered from these few birds can be used to guide further investigations on presumably important sites, saving effort and money from labourious field expeditions with sometimes uncertain outcomes.

Dark-bellied brent geese *Branta bernicla bernicla* (hereafter brent) breed in high arctic Russia, predominantly on the Taymyr Peninsula (Bergmann, Stock & ten Thoren 1994, van Nugteren 1997, Syroechkovski Jr & Litvin 1998, Ebbing, Berrevoets, Clausen, Ganter, Günther, Koffijberg, Maheo, Rowcliffe, St. Joseph, Südbek & Syroechkovsky 1999). Their winter area stretches from the Danish part of the Wadden Sea to France and England. During spring migration almost the entire population gathers in the Wadden Sea between March and late May to build up nutrient stores for the coming spring migration. In late May-early June the geese leave western Europe for a 2,500 km flight to the region of the White Sea and the Kanin Peninsula, northwest Russia. The White Sea and the west side of the Kanin Peninsula are crucial intermediate stopover areas during spring migration (Ebbing & Spaans 1995, Syroechkovski Jr & Litvin 1998, Ebbing et al. 1999, Drent et al., unpubl. data). In mid-June they continue a further 2,500 km to the breeding areas, usually without any longer stopovers (Syroechkovski Jr & Litvin 1998). Non-breeding birds may, however, use intermediate stopovers between the White Sea and Taymyr and arrive 1-2 weeks later than breeding birds (Green et al. 2002).

In autumn, the birds leave Taymyr in late August-early September and arrive in the Wadden Sea in late Sep-

tember to mid-October. According to Syroechkovski Jr & Litvin (1998) brent in general use more stopover areas along the coast of the Arctic Ocean during autumn than during spring. Despite being one of the most well-studied populations migrating along the East Atlantic Flyway, there is still limited knowledge about the part of migration taking place within Russia, along the coast of the Arctic Ocean.

In this article, we present data on the summer and autumn localities used by the satellite-tracked brent. We also analyse migration performance during the initial part of autumn migration for these birds. We compare migration performance and site use in autumn with data gathered for the same individuals during spring migration, and we investigate whether brent conduct autumn migration in the same way as spring migration. We also give an update on known stopover areas along the coast of the Arctic Ocean, evaluate the relative importance of different stopover areas in spring and autumn and give an overview of the present legal status of these areas.

Methods

In spring 1999, we supplied eight adult male brent with Microwave Telemetry Inc. 30 g PTTs (Platform Transmitter Terminals) in the Netherlands. The six birds tracked during summer (five of these also during

autumn) were caught on the island of Terschelling (53°26'N, 5°30'E) in May 1999. All the PTTs were programmed with a continuous transmission cycle of 10 hours ON and 13 hours OFF, running until battery exhaustion. A more detailed description of the methods used is given in Green et al. (2002). The birds were also marked with individually recognisable combinations of colour rings that enabled recognition in the field. For ease of comparison the birds in this article are identified by letters being the same as those presented in Green et al. (2002).

We received 1-28 positions per day during the stay at breeding/moulting areas at Taymyr and during autumn migration. Generally the number of received positions per day decreased during the last week before the batteries ran out of power. Data handling and selection of positions follow Green et al. (2002). In our analysis of breeding/moulting- and stopover areas we have used only high-class positions with an estimated accuracy of <1 km. We have divided stops during migration into long-time and short-time stopovers (Green et al. 2002). Stops exceeding 48 hours were classified as long-time stopovers and those lasting less than 48 hours as short-time stops. The basis for this division is that we find it more likely that stops exceeding 48 hours are fuelling stopovers with the possibility of a net energy gain for the birds, whereas this is unlikely for birds staying less than 48 hours.

The data collected by satellite telemetry were supplemented with data from readings of colour rings in the wintering area in order to establish whether the birds actually completed autumn migration.

Results

Site use during the summer

After arrival at Taymyr in late June-early July several of the birds made some shorter movements within the peninsula before they settled for the summer (Green et al. 2002), and the localities where the birds remained stationary for most of the summer, after the early summer movements, are shown in Figure 1. Birds A and E both stayed inland on the northern part of the peninsula at the Tolevaya river (75°39'N, 93°05'E). Bird A remained in that area during 1 July - 25

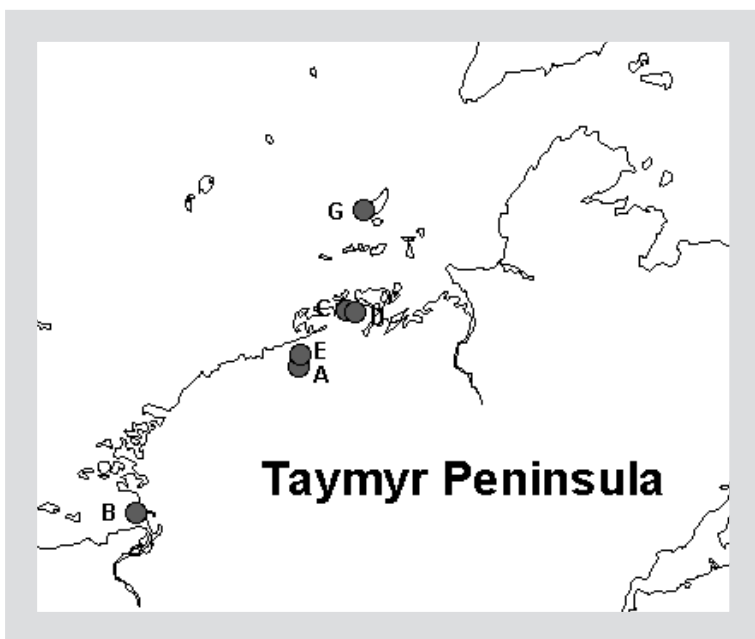


Figure 1. Localities on the Taymyr Peninsula where six dark-bellied brent geese remained stationary during the summer of 1999, as recorded by satellite telemetry. The letters refer to the different individuals.

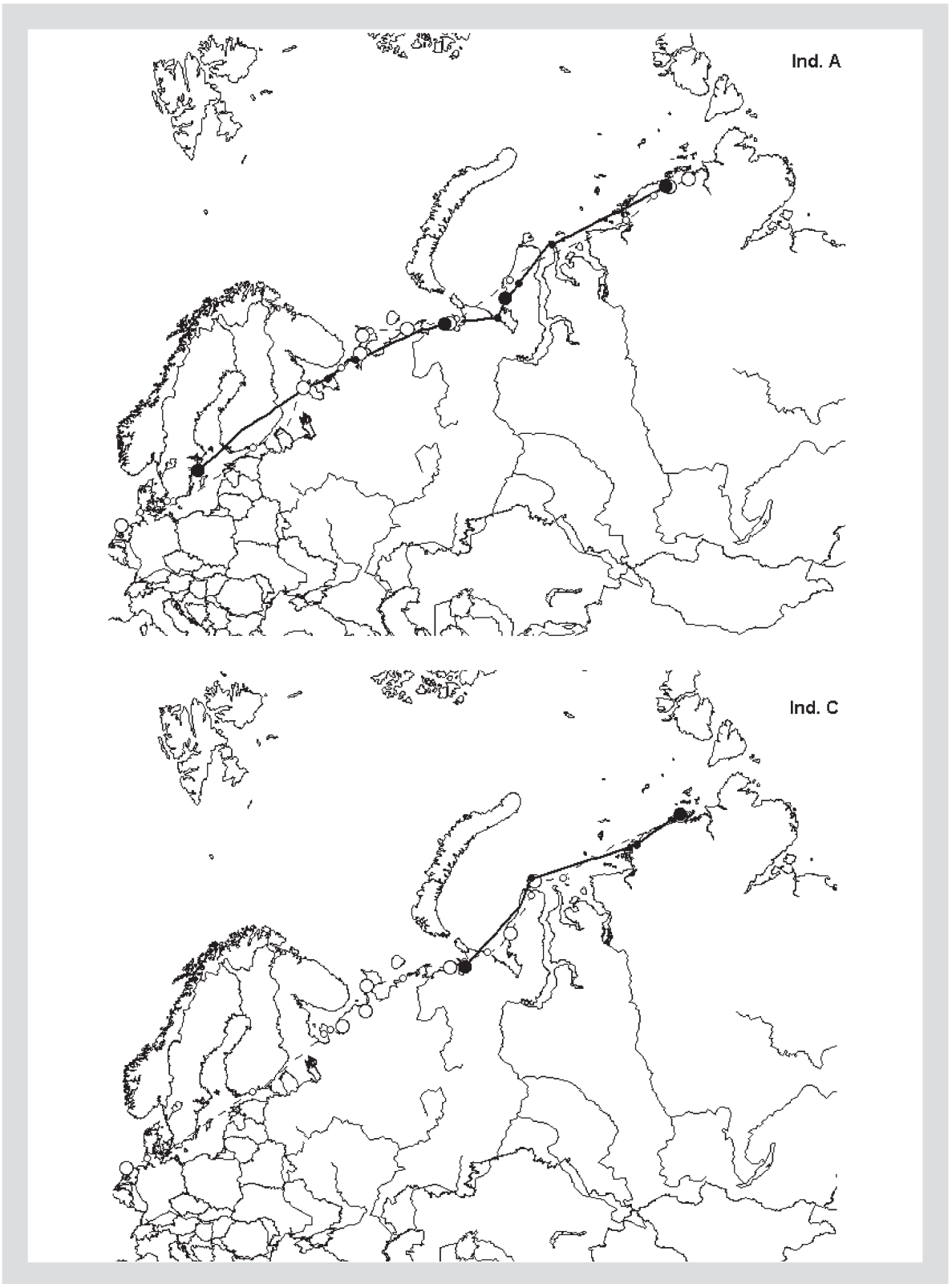


Figure 2. Autumn (bold line, ●) and spring (broken line, ○) tracks of five adult male dark-bellied brent geese in 1999. The large circles show long-time stopovers (>48 hours) and small circles show short-time stopovers (<48 hours).

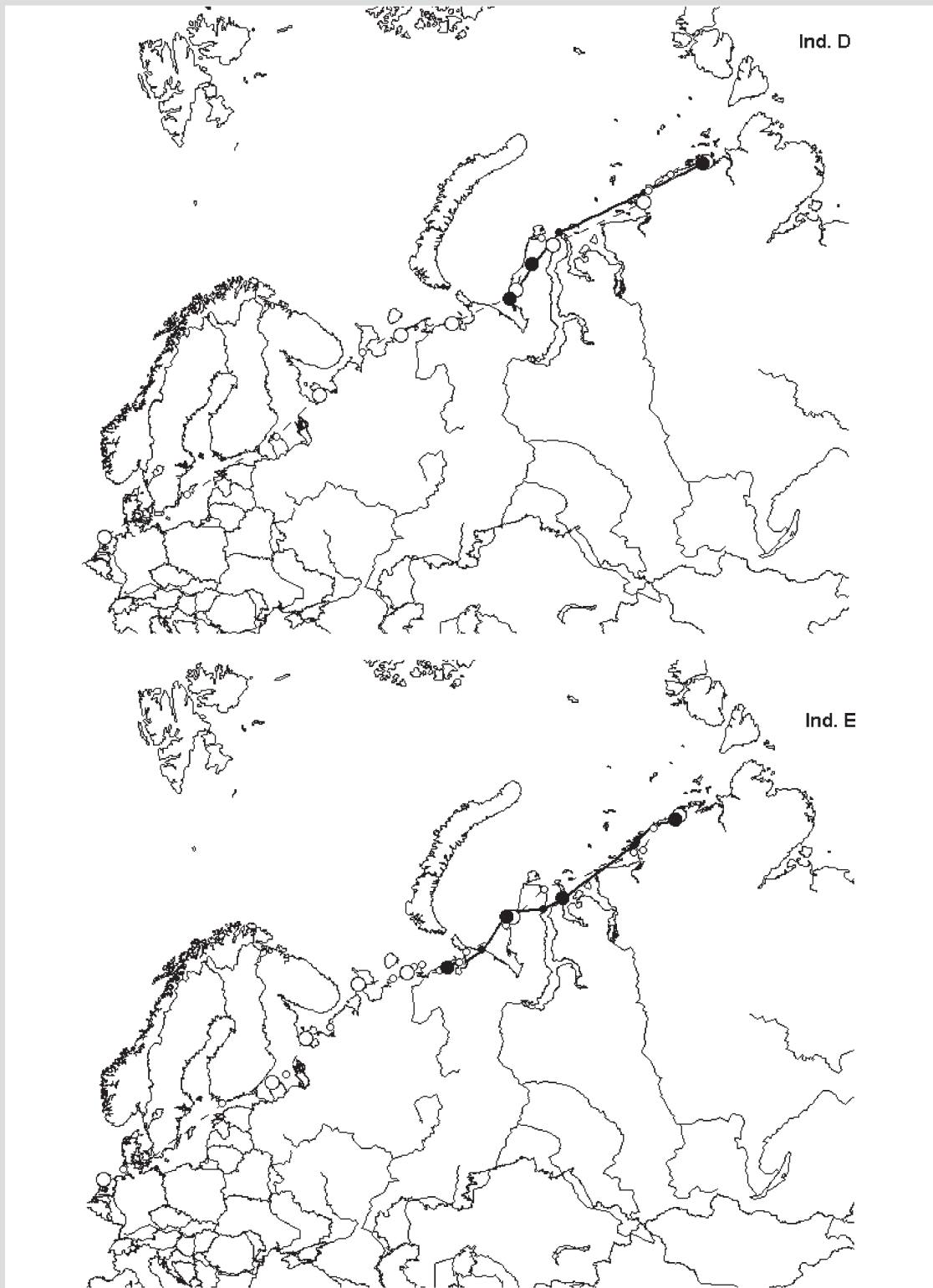


Figure 2. ... continued



Figure 2. ... continued

August, while bird E stayed there during 9 July - 16 August. Bird B spent the summer on an island in the Pyasina delta ($74^{\circ}2'N$, $86^{\circ}39'$). It arrived there on 7 July and was still on the island when the battery ran out of power on 15 August. The summer localities of birds C and D were situated on the northern coast. Bird C stayed south of Nansen Island ($76^{\circ}04'N$, $94^{\circ}53'E$) during 8 July - 25 August, while bird D stayed south of Taymyr Island during 8 July - 26 August ($76^{\circ}11'N$, $95^{\circ}38'E$). Finally, bird G stayed at Russkiy Island, Nordenskiöld archipelago ($77^{\circ}00'N$, $95^{\circ}35'E$) for most of the summer, i.e. 8 July - 31 August. Before starting autumn migration proper it moved to Petersen Island, still in the Nordenskiöld archipelago ($76^{\circ}41'N$, $95^{\circ}56'E$), and stayed there during 1-5 September. The average length of stay at the summer localities, i.e. the period during which no longer movements could be detected, was 48 days (± 7.5 days (SD); $N = 5$).

Routes and migratory performance during autumn

The routes for the five birds recorded during parts of the autumn migration compared to the spring migration

routes for the same birds are shown in Figure 2. Despite the similarity of the routes between birds, none of the birds migrated together with any other satellite-tracked bird in either season. The figures include positions until the transmitters ran out of battery power and do not show complete migration routes to the winter destinations. Tracking distances during autumn migration were roughly between 20 and 75% of the expected total migration distance from breeding to wintering areas ($>5,000$ km).

Four of the five birds tracked during autumn migration were subsequently recorded (readings of colour rings) in the wintering and spring-staging area in the Wadden Sea (birds A, C, D and E). Also bird B, which was tracked during spring migration and the summer until the battery failed on 15 August, was seen in the Wadden Sea during the following winter and spring season. All five birds actually returned to the island of Terschelling, where they originally had been caught, for shorter or longer stays. Thus, at least five of the six birds that completed spring migration did also complete a successful autumn migration. None of the birds returning to the wintering area were accompanied by juveniles,

Table 1. Summary statistics of the initial part of autumn migration for five adult male, dark-bellied brent geese during 1999, as recorded by satellite telemetry. End date shows the date when the transmitters stopped functioning, not the date when the birds reached their destinations. Total distance refers to tracking distance, not the total distance to the wintering area. Overall migration speed was calculated from the date of departure from the breeding/moulting area to arrival at the last stopover site during the time the transmitters worked. The overall migration speed of bird C is given in parentheses because the transmitter stopped functioning just after arrival at the first staging site, making the calculated migration speed incomparable with those of the other birds.

Bird ID	Departure date	End date	Total distance (km)	No. of flights	Mean flight (km)	Longest flight (km)	No. of stopovers > 48 hours	No. of stopovers < 48 hours	Overall migration speed (km/day)
A	25 Aug	25 Sept	3751	8	469	1331	3	5	134
C	25 Aug	29 Aug	1472	3	491	655	2	1	(368)
D	27 Aug	9 Sept	1150	3	383	715	2	1	128
E	17 Aug	6 Oct	1622	6	270	431	3	3	74
G	5 Sept	5 Oct	1602	6	267	775	2	4	84

indicating that none of them had bred successfully. This was disappointing, because 1999 was a good breeding season (Volkov, Khomenko, van Kleef & Willems 2000).

The geese departed from Taymyr in late August - early September (Table 1), the median departure date being 25 August. The birds flew long distances without any longer stops (651-1,550 km; mean: 1,125 km \pm 379 km (SD); N = 5) directly from their summering sites. All birds used several stopovers along the route and overall mean flight length was 376 km for the recorded part of autumn migration. The longest flights made by the birds averaged 781 km.

Site use in spring and autumn

Individual site use during spring and autumn migration (spring data from Green et al. 2002) is shown in Table 2. We use site in a wider meaning, corresponding to a larger, general area rather than a discrete, small-scale

site. The distribution of stopover areas is shown in Figure 3. Looking primarily at the areas where long-time (fuelling) stops were made, all birds showed some degree of site fidelity, as all to a varying extent returned to areas used during the preceding spring also for autumn stopovers. At the same time there was a great deal of variation as all birds used at least some sites for longer stops only in spring or in autumn. Dividing the localities in Table 2 into three categories covering i) sites used by the same bird in both seasons, ii) sites used by the individual bird only in spring, and iii) sites used by the bird only during autumn showed that especially sites 6 and 8 were used by several birds for longer stops in both spring and autumn, whereas sites 1-5 and 9-10 were mostly used in spring and sites 7 and 11 were mostly used in autumn. However, from the more westerly sites (1-5) we only received data from one single bird during autumn migration.

Table 2. Comparison of stopover site use (in no. of bird days) during spring and autumn migration for each of five dark-bellied brent geese in 1999, and of overall stopover site use between spring and autumn migration for eight dark-bellied brent geese as recorded by satellite telemetry during 1998-1999 (the last two columns to the right). The figures in the two columns show the average number of bird days/birds passing the site. The N-values in parentheses show how many satellite-tagged birds have passed the sites. Spring data for birds A-G given in italics are from Green et al. (2002). For a reference of stopover site numbers see Figure 3. In the table s indicates a short stop (< 48 hours) and results for one individual tracked during spring 1998 are also included (see Green et al. 2002).

Stopover site	Bird A		Bird C		Bird D		Bird E		Bird G		No. of bird days		
	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	
1. Onega Bay, White Sea		2	<i>s</i>	-	<i>4</i>	-	<i>8</i>	-	<i>s</i>	-	<i>2.4 (8)</i>	<i>0 (1)</i>	
2. Dvina Bay, White Sea			<i>s</i>	2	-	-	<i>s</i>	-	-	-	<i>2.8 (7)</i>	<i>1 (1)</i>	
3. Mezen Bay, SW Kanin Peninsula		7	<i>s</i>	7	-	-	-	-	-	-	<i>2.0 (7)</i>	<i>1 (1)</i>	
4. W Kanin Peninsula		7	<i>16</i>	-	<i>s</i>	-	<i>8</i>	-	-	-	<i>6.7 (7)</i>	<i>0 (1)</i>	
5. Sengveyskiy Island - Kolokolkova Bay		5	<i>s</i>	-	7	-	7	-	7	-	<i>4.0 (7)</i>	<i>0 (1)</i>	
6. Pesyakov Island - Khaypudyrskaya Bay		4	11	5	>2	14	-	<i>s</i>	20	12	22	7.1 (7)	13.8 (4)
7. Torasovay Island - Amderma			<i>s</i>							<i>s</i>	3	<i>0.4 (7)</i>	<i>1.7 (3)</i>
8. W Yamal Peninsula		<i>s</i>	13	4		5	5	5	2	2	<i>s</i>	<i>3.9 (7)</i>	<i>4.2 (5)</i>
9. NE Yamal Peninsula				<i>s</i>		4		<i>s</i>	<i>s</i>			<i>1.5 (6)</i>	<i>0 (5)</i>
10. Bely Island				8	<i>s</i>							<i>4.0 (2)</i>	<i>1.0 (1)</i>
11. Yavay Peninsula - Vilkitskogo Island			<i>s</i>	<i>s</i>			<i>s</i>		10	<i>s</i>		<i>1.3 (6)</i>	<i>2.4 (5)</i>

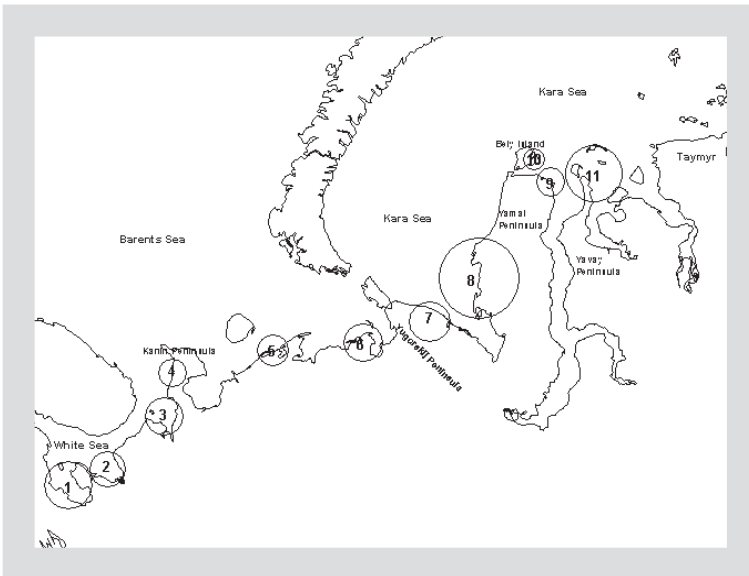


Figure 3. Stopover areas (encircled) used by satellite-tracked dark-bellied brent geese during spring and autumn migration 1999. The numbers refer to the stopover sites give in Tables 2 and 3.

If we evaluate site use by considering the number of bird days per site per bird actually shown by satellite tracking to have passed through the area in question, a similar pattern emerges (see Table 2). Sites 1-5 and 10 were used for longer stops during spring, sites 6 and 8 were used for longer stops during both spring and autumn, and sites 7, 9 and 11 were mainly used for shorter stops.

Discussion

The possible effects on bird behaviour caused by the carrying of transmitters are discussed in detail in Green et al. (2002). Our conclusion from both the spring and autumn migrations of these individuals is that in most aspects bird behaviour was perfectly normal (e.g. general timing of migration, routes taken), but we cannot rule out the possibility that carrying an external equipment made the geese decide to forego breeding in 1999 and thus conduct the later stages of spring migration at a slightly lower pace than birds heading for a breeding attempt.

Routes and migration performance

The routes taken by the birds during autumn migration were very similar to those recorded during spring migration, but of course in the reversed direction. Even at a very fine scale, individual birds, perhaps with the exception of bird D, followed nearly identical routes in autumn as they did during the preceding spring e.g. when crossing land (see Fig. 2). At a larger scale, all birds fol-

lowed the coast of the Arctic Ocean southwestwards from the Taymyr Peninsula. As shown by Green et al. (2002) this route is about 16% longer than the shortest route, the great circle (orthodrome), to the wintering areas in western Europe. Probably, the longer route actually taken by the birds could have other benefits such as good opportunities to find food, fresh water and shelter compared to the shorter route, the great circle, which would take the birds over the Arctic Ocean. In addition, the longer route is probably also easier from an orientational point of view as the birds can use the coastline as a leading line (Green et al. 2002). The recorded migration routes and the timing of the autumn migration in our study generally fit previous descriptions based on field observations very well (Bergmann et al. 1994, van Nugteren 1997, Syroechkovski Jr & Litvin 1998), although these authors comment that the migration corridor may be wider in autumn than in spring, something that we could not find in the satellite-tracked birds.

General migration performance was also very similar between spring and autumn migration with relatively short flights alternating with longer or shorter stops. Average flight distances for the tracked part of autumn migration (267-491 km) were intermediary between the corresponding values for the first half of spring migration (Wadden Sea - Kanin Peninsula: 362-733 km; Green et al. 2002) and the latter half of spring migration (Kanin - Taymyr: 160-289 km; Green et al. 2002). Also the average longest flight during autumn was very similar to the corresponding value for spring migration. Average migration speeds, including time spent at stopovers were roughly in the same range during autumn migration (74-134 km/day) as during spring migration (97-148 km/day; Green et al. 2002).

We thus conclude that autumn migration can be interpreted as an almost exact reverse process of spring migration, regarding routes taken and general performance. It must be kept in mind though that this pattern recorded by satellite tracking refers to non-breeding birds, and it is very likely that birds heading for a breeding attempt in spring and birds bringing back juveniles (successful breeders) in autumn behave somewhat differently. The latter category of birds probably use fewer stopovers and conduct migration at a slightly higher pace in spring,

especially during the later stages (Syroechkovski Jr & Litvin 1998) than non-breeders. In autumn, both dark-bellied and light-bellied brent have been shown to arrive later at the wintering areas in good breeding years than in non-breeding years (Prokosch 1984, Clausen & Fisher 1994), indicating a slower speed of migration for successful breeders than for non-breeders.

Site use during summer

We could not decide with absolute certainty whether our birds attempted to breed or chose to forego breeding altogether. The late arrival at the breeding grounds (Green et al. 2002), the many movements within Taymyr during the initial part of the summer and the finding that none of these individuals returned to the wintering area with juveniles make it likely that they did not even try to breed in 1999. The sites used during summer can thus probably be regarded primarily as moulting sites. Among the sites used during summer, only the Pyasina delta is a known larger moulting area (>10,000 birds; Ebbinge et al. 1999). Whether the other areas also hold larger numbers of moulting brent remains to be shown. All the localities are, however, known breeding sites for brent (*cf.* figure 20.3 in Ebbinge et al. 1999). The localities used during summertime were all situated within protected areas (Great Arctic Reserve, designated in 1993).

The brent start moulting in mid-July and the flight feathers take about 40 days to be fully regrown (Cramp 1977, Bergmann et al. 1994). The fact that the birds remained stationary at the same sites until the start of autumn migration and that the duration of stay at these sites exceeded the time needed for completion of flight-feather moult by on average only a week, has two implications. First, the moulting sites apparently also function as pre-migratory staging sites, where build-up of fuel stores for the first part of autumn migration takes place. Secondly, as the birds flew rather long distances without any longer (fuelling) stops directly from their summering sites, they have to build up relatively large fuel stores before the start of autumn migration. The average initial flight, before the first longer stop, corresponds to about 16 hours of flight, assuming an average groundspeed of 70 km h^{-1} (19 m s^{-1} ; Green & Alerstam 2000), or about 22% of the total migration distance. The build-up of necessary fuel stores to cover this distance can apparently be made simultaneously with the later stages of flight-feather moult. This behaviour is in contrast to findings regarding the Spitsbergen barnacle geese *Branta leucopsis*, for which Butler, Woakes & Bishop (1998) indicate that individuals followed by satellite telemetry moved a shorter distance following the moult to final staging (fuelling) sites before embark-

ing on a long flight over the Arctic Ocean towards Bear Island and the Norwegian coast.

Site use during spring and autumn migration

Stopover sites were not used in any simple orderly way, with a chain of sites used during spring migration by all birds and then used again in the reversed order in autumn. Despite the fact that all birds made at least one long stopover (>48 hours) during autumn migration in an area where they made a long stop in spring, the overall picture in site use was one of considerable variation both between individuals but also within individuals between seasons. Thus we conclude that brent migration along the coast of the Arctic Ocean is more complex than just a simple migration system where a few key sites are used (*cf.* examples in Davidson & Stroud 1996). Instead brent seem to use a multitude of localities, where the use of any single site may differ between individuals and seasons. The pattern obtained is similar to what has been found in western sandpipers *Calidris mauri* migrating along the Pacific North American coast (Iversen, Warnock, Butler, Bishop & Warnock 1996) and might be more common among several waterfowl species (*cf.* Farmer & Wiens 1998, Haig et al. 1998) than previously recognised. From a conservation point of view this means that safeguarding only a few sites may not fulfil the requirements for long-distance migratory populations. Even within seemingly highly synchronised populations (such as brent populations) there may be considerable variation in how and when different sites are used. In this context it is worth noting the recent findings of Pettifor, Caldwell, Rowcliffe, Goss-Custard, Black, Hodder, Houston, Lang & Webb (2000), who approached the consequences of habitat or site loss to the size of the brent population. The system they modelled was wintering sites and their spatial configuration in relation to the main spring staging area (the Wadden Sea). They predicted that destruction (removal) of wintering sites leading to an increase in distance between wintering and spring staging areas had more adverse effects on population size than removal of sites not resulting in such an increase in migratory distance. If their predictions from the wintering sites hold true for the whole range of sites the brent currently use, this highlights that safeguarding a chain of localities along the migration route, in order to minimise flight distance between main staging and breeding areas, most likely is of higher conservation importance than focusing on sites at the edges of the current distribution range if present population size is going to be unaffected.

Several of the sites used for longer stops during migration by the satellite-tracked birds were previously

Table 3. Literature data on the importance of the stopover areas used by satellite-tracked brent during spring and autumn and the legal protective status of the respective areas. Data are from a) van Nugteren (1997), b) Syroechkovski Jr & Litvin (1998), c) Ebbinge et al. (1999) and d) Lorentsen et al. (1998). The spring and autumn columns show the maximum recorded numbers existing; when no exact data exist a general evaluation based on the above-mentioned sources are shown. Lack of data in the spring and autumn columns means that these sites have not been recognised as important stopover sites in the literature. For a reference to site numbers see Figure 3.

Stopover site	Spring	Autumn	Protective status
1. Onega Bay, White Sea	Thousands ^{a)}	100 000 ^{c)}	None
2. Dvina Bay, White Sea	30 000 ^{c)}	Important ^{b)}	None
3. Mezen Bay, SW. Kanin Peninsula	Thousands ^{c)}	Important ^{b)}	None
4. West Kanin Peninsula	Tens of thousands ^{a)}	Tens of thousands ^{a)}	State Nature Reserve Shoininski ^{d)}
5. Sengeyskiy Island - Kolokolkova Bay	Thousands ^{a)}	Important ^{b)}	None
6. Pesyakov Island - Khaypudyrskaya Bay		Important ^{b)}	None
7. Torasovay Island - Amderma			None
8. West Yamal Peninsula	Tens of thousands ^{a)}	Tens of thousands ^{a)}	None
9. North-east Yamal Peninsula			None
10. Bely Island			None
11. Yavay Peninsula - Vilkitskogo Island	Tens of thousands ^{a)}	Tens of thousands ^{a)}	Gydansky Strict Nature Reserve

known to be of great importance for this population. Our findings strongly underline the importance of the White Sea area in spring (Ebbinge & Spaans 1995, Clausen 1997, Syroechkovski Jr & Litvin 1998, Ebbinge et al. 1999). Also for the Kanin Peninsula area our data are in agreement with earlier findings that this area is crucial during spring migration (Syroechkovski Jr & Litvin 1998). During autumn none of these areas were used for longer stops by the only bird we could track that far west, which is at odds with reported large autumn concentrations of brent in this area in other years (Ebbinge et al. 1999). A possible explanation may be that the use of the White Sea in autumn may vary considerably between individuals and seasons.

Further east, the satellite-tagged birds used mainly three areas for longer stays (see Table 2). The Sengeyskiy Island-Kolokolkova Bay (Tobseda) area has previously been recognised as an important autumn stopover area (Syroechkovski Jr & Litvin 1998), but our study implies that it also may be important during spring migration. The Pesyakov Island-Khaypudyrskaya Bay area has not been recognised as an important stopover area at all before. For the satellite-tracked birds this was the area in which they spent the longest time both during spring and autumn (see Table 2). Based on these findings we conclude that the Pesyakov Island - Khaypudyrskaya Bay may function as an important spring board, perhaps with its greatest importance during autumn migration. That the west side of the Yamal Peninsula was used by several birds both during spring and autumn agrees well with literature data on the importance of this area (Syroechkovski Jr & Litvin 1998).

One may argue that the site use by a few satellite-tracked birds may not reflect the general behaviour of the population, but in our view our results correspond so well with existing literature data that we feel confident to pin-point the sites mentioned above as potentially

very important stopover sites. Given the difficulties in conducting field work in these areas, it might be wise to use the existing satellite-tracking data to guide further efforts of evaluating the importance of these sites. Spring staging of brent has been studied at one site in the White Sea (Dry Sea, Dvina Bay) so far in order to understand the role of this area in the annual movements of brent and to get detailed data on numbers using the area, feeding ecology and potential anthropogenic threats (Clausen 1997; Drent et al., unpubl. data). From all other areas mentioned above such data are lacking. As few of these have any formal legal protection today (Table 3) it would be of great value if similar data were collected also from these areas if the objectives of the Flyway Management Plan of dark-bellied brent geese (van Nugteren 1997) should be fulfilled, i.e. "to seek the conservation of sufficient natural coastal habitats to support the population throughout its flyway".

Acknowledgements - this study was financed by the Gratama Stichting and the Stichting Groninger Universiteitsfonds (grants to Rudi Drent), and by the Swedish Natural Science Research Council (grant to Thomas Alerstam). We also thank Gerhard Müskens, Jan Ellens and Harry Hoorn for their help in the catching actions and in the case of Jan and Harry also for devoted ring-reading on Terschelling.

References

- Alerstam, T. 1979: Wind as a selective agent in bird migration. - *Ornis Scandinavica* 10: 76-93.
- Bergmann, H-H., Stock, M. & ten Thoren, B. 1994: Ringelgänse. - AULA-Verlag, Wiesbaden, 251 pp. (In German).
- Butler, P.J., Woakes, A.J. & Bishop, C.M. 1998: Behaviour and physiology of Svalbard Barnacle Geese *Branta leucopsis* during their autumn migration. - *Journal of Avian Biology* 29: 536-546.

- Clausen, P. 1997: Dark-bellied Brent Geese *Branta b. bernicla* use of the White Sea. A progress report. - In: van Nugteren, J. (Ed.); Flyway Management Plan of Dark-bellied Brent Goose *Branta bernicla bernicla*. Wageningen 1997, pp. 174-183.
- Clausen, P. & Fischer, K. 1994: Lysbuget knortegås *Branta bernicla hrota*: Forekomst og økologi i Vadehavet. (In Danish with English summary: Light-bellied Brent Goose (*Branta bernicla hrota*): Occurrence and ecology in the Danish Wadden Sea. - Dansk Ornithologisk Forenings Tidsskrift 88: 9-22.
- Cramp, S. (Ed.) 1977: Birds of the Western Palearctic. - Oxford University Press, Oxford, 722 pp.
- Davidson, N.C. & Stroud, D.A. 1996: Conserving international coastal habitat networks on migratory waterfowl flyways. - Journal of Coastal Conservation 2: 41-54.
- Davidson, N., Bryant, D. & Boere, G. 1999: Conservation uses of ringing data: flyway networks for waterbirds. - Ringing & Migration 19 (suppl.): S83-94.
- 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. - Journal of Avian Biology 26: 105-113.
- Ebbinge, B., Berrevoets, C., Clausen, P., Ganter, B., Günther, K., Koffijberg, K., Maheo, R., Rowcliffe, M., St. Joseph, A.K.M., Südbeck, P. & Syroechkovsky Jr, E.E. 1999: Dark-bellied Brent goose (*Branta bernicla bernicla*). - In: Madsen, J., Cracknell, G. & Fox A.D. (Eds); Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International Publ No. 48, Wetlands International, Wageningen, The Netherlands, National Environmental Research Institute, Rønde, Denmark, pp. 284-297.
- Farmer, A.H. & Wiens, J.A. 1998: Optimal migration schedules depend on the landscape and the physical environment: a dynamic modeling view. - Journal of Avian Biology 29: 405-415.
- Glahder, C.M., Fox, A.D. & Walsh, A.J. 1997: Effects of fitting dummy satellite transmitters to Greenland white-fronted geese *Anser albifrons flavirostris*. - Wildfowl 48: 88-97.
- Green, M. & Alerstam, T. 2000: Flight speeds and climb rates of Brent Geese: mass-dependent differences between spring and autumn migration. - Journal of Avian Biology 31: 215-225.
- Green, M., Alerstam, T., Clausen, P., Drent, R. & Ebbinge, B.S. 2002: Dark-bellied Brent Geese *Branta bernicla bernicla*, as recorded by satellite telemetry, do not minimize flight distance during spring migration. - Ibis 144: 106-121.
- Haig, S.M., Mehlman, D.W. & Oring, L.W. 1998: Avian movements and wetland connectivity in landscape conservation. - Conservation Biology 12 (4): 749-758.
- Iversen, G.C., Warnock, S.E., Butler, R.W., Bishop, M.A. & Warnock, N. 1996: Spring migration of Western Sandpipers along the Pacific coast of North America: a telemetry study. - Condor 98: 10-21.
- Lorentsen, S-H., Jostein Öien, I. & Aarvak, T. 1998: Migration of Fennoscandian Lesser White-Fronted Geese *Anser erythropus* mapped by satellite telemetry. - Biological Conservation 84: 47-52.
- Pettifor, R.A., Caldow, R.W.G., Rowcliffe, J.M., Goss-Custard, J.D., Black, J.M., Hodder, K.H., Houston, A.I., Lang, A. & Webb, J. 2000: Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. - Journal of Applied Ecology 37 (Suppl. 1): 103-135.
- Prokosch, P. 1984: Population Jahresrythmus und traditionelle Nahrungsplatzbindungen der Dunkelbäuchigen Ringelgans (*Branta b. bernicla*) im Nordfriesischen Wattenmeer. (In German with English summary: Population, Annual Cycle and traditional Relationships to Feeding Areas of the Dark-bellied Brent Goose (*Branta bernicla bernicla*, L. 1758) in the Northfrisian Waddensea. - Ecology of Birds 6: 1-99.
- Syroechkovski Jr, E.E. & Litvin K.E. 1998: Migrations of Brent Geese (*Branta bernicla bernicla*) in Russia. - Casarca 4: 71-95. (In Russian with English summary).
- van Nugteren, J. (Ed.) 1997: Flyway Management Plan of Dark-bellied Brent Goose *Branta bernicla bernicla*. - Wageningen 1997, 198 pp.
- Volkov, A.E., Khomenko, S., van Kleef, H. & Willems, F. 2000: Breeding of brent geese at Meduza Bay, Taimyr, and relation with lemming predators. - Casarca 6: 63-75.