Non-stop autumn migrations of Light-bellied Brent Geese *Branta bernicla hrota* tracked by satellite telemetry – racing for the first *Zostera* bite?

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Abstract

Satellite telemetry tracking of Light-bellied Brent Geese was used to test whether the length of time taken to undertake their autumn migration was longer than the duration of their spring migration (published previously). Spring and autumn migration did not differ significantly and both were conducted almost non-stop, despite expectations that birds would be more time-limited in spring than autumn. Rich feeding opportunities in the arctic prior to autumn departure and large beds of eelgrass *Zostera* sp. at the final destinations, combined with a lack of suitable *Zostera* feeding habitat at potential staging areas along the route, most likely explain the rapid and direct autumn migration pattern observed in the population. Although individual goose migrations were fast and of similar duration in the two seasons, autumn migration for the entire population was spaced over a month, in contrast to spring when all birds usually migrated within a 10-day period. From the lack of a difference between tagged and non-tagged individuals in the timing of their migration (the latter based on citizen science observation phenology), we believe the birds' movements were largely unaffected by their tags.

Key words: foraging stopovers, migration strategy, satellite telemetry, time minimiser, *Zostera*.

Several factors limit the ability of long-distance migratory birds to move between their winter quarters and breeding sites, including time, predation risk and deposition of the fat stores needed to fuel the long flight (Alerstam 2011). Migration strategies therefore have been proposed which may involve minimising the time needed to complete migration, the energy expenditure involved, and the mortality risk to the birds (Alerstam & Lindström 1990). To maximise fitness, long-distance migrants should minimise spring migration duration to arrive earliest at their breeding sites (Moore *et al.* 2005), in the best possible condition for securing and defending prime breeding

territories (Kokko 1999), and this strategy has been described for many avian species (Nilsson *et al.* 2013). Early nesting results in larger clutch sizes and better quality offspring, more likely to survive their first migration (Perrins 1970; Rowe *et al.* 1994; McNamara *et al.* 1998). This therefore predicts that spring migration in long-distance migratory geese would be faster than in autumn, especially because, after a summer of biological productivity, food resources are abundant and the need to reach the wintering grounds by a certain date is less crucial than the fitness imperative of early arrival in spring to start breeding.

Previous studies of migratory goose populations have however shown conflicting patterns in the relative duration of their spring and autumn migrations. The Swan Goose *Anser cygnoides* and the eastern population of Greylag Goose *Anser anser*, which both have a relatively short distance migration between breeding areas in Mongolia and wintering sites in China, conform to the hypothesis by undertaking spring migration almost twice as rapidly as on covering the same distance in autumn (Batbayar *et al.* 2013; Li *et al.* 2020a). In contrast, for the Bar-headed Goose *Anser indicus* (also a short-distance migrant, flying between breeding areas in Kyrgyzstan and wintering sites in Pakistan, India and Uzbekistan), the spring and autumn migrations are of equal duration (Köppen *et al.* 2010). Moreover, some longer-distance, arctic-nesting species, such as the Greater White-fronted Goose *Anser albifrons* which migrates between winter quarters in western European and the Russian arctic breeding

areas, take almost twice as long to complete migration in spring (83 days) than in autumn (42 days; Kölzsch *et al.* 2016). Other goose populations show a similar pattern, with migration taking longer in spring than in autumn, due to prolonged time spent at spring stopover sites (*e.g.* Deng *et al.* 2019; Li *et al.* 2020b). As well as females accumulating body stores for investment in clutches and for self-maintenance during incubation, many arctic-nesting waterbirds may be delayed on spring migration by encountering adverse weather during their journeys north, factors less likely to limit the timing of their southbound migration in autumn (*e.g.* Evans 1982; Nuijten *et al.* 2014; Li *et al.* 2020b). Sympatric wintering Tundra Bean Geese *Anser serrirostris* breeding in different parts of the Russian high arctic thus migrate at speeds determined by the rate of thaw along their allopatric flyways, including at their ultimate breeding areas. As a result, despite simultaneous departure, birds flying 1,000 km further to their breeding sites arrived 23 days earlier than those undertaking the shorter migration, but both groups of birds arrived at their respective breeding areas 8–9 days ahead of local 50% snow thaw, suggesting that this was the optimal arrival time for breeding (Li *et al.* 2020b).

Increasingly, it is recognised that arctic-breeding female geese accumulate energy and nutrient body stores at staging areas during spring migration, to add to exogenous resources exploited close to their ultimate breeding territories on arrival at the breeding grounds (Gauthier *et al.* 2003; Drent *et al.* 2006). As a result, they tend to be situated towards the capital end of the

gradient between the so-called "capital" and "income" investment in breeding described by Drent & Daan (1980). The accessibility of this food in spring is determined by the timing of the vernal thaw and onset of above-ground primary production of graminoid food plants utilised by the geese (described as a "green wave" by Drent *et al.* 1978; Owen 1980), which may vary considerably from year to year. It now appears that relatively few arctic-nesting geese strictly follow the "green wave" of early above-ground plant production along their respective spring flyways (Wang *et al.* 2019). However, the quality and availability of such resources for breeding females during spring migration will affect their ability to put on the energy and nutrient stores required for reproduction (*e.g.* Drent *et al.* 2006; Hübner *et al.* 2010).

The question therefore arises as to how females in an arctic-nesting goose population, with little or no opportunity for refuelling along its migration route, can develop the nutrient stores needed to breed successfully. In this case, we might expect that where geese are constrained to fly uninterrupted over the same inhospitable terrain in both spring and autumn then, given similar meteorological conditions, the duration of spring migration would likely be equal to that of autumn. We predict this despite the expectation that the northbound flight in spring should be more rapid than autumn migration, under the minimising time spent on spring migration hypothesis, because the birds have no choice about staging in terrestrial habitats along the route. Migration duration, both to and from the breeding grounds, therefore should simply

be the time that it takes to fly the distance involved.

The East Atlantic population of the Light-bellied Brent Goose *Branta bernicla hrota* migrates almost exclusively across open sea, from breeding areas in Svalbard and northeast Greenland to wintering sites in Denmark and at Lindisfarne in northeast England (Denny *et al.* 2004). The short arctic summer constrains the timing of the breeding season, so that the geese must arrive on their territories, breed, moult and depart on their southbound migration before the onset of winter (Klaassen 2003). For this reason, Brent Goose spring migration would be expected to be time-limited, a view supported by observations of largely uninterrupted spring migration direct from the winter quarters to the nesting areas (Clausen & Bustnes 1998; Clausen *et al.* 2003).

While the importance of early arrival to maximise breeding success seems to be a main driver of the timing of spring migration, autumn migration might be less influenced by time constraints, as illustrated by the relatively long autumn migration periods recorded for some passerine species (Fransson 1995; Yohannes *et al.* 2009), as well as by the goose examples mentioned above. The timing of arrival at the wintering grounds presumably has little effect on subsequent survival and reproductive success, so is not under such severe selection pressure. Consequently, if the main cost of late arrival is depleted food resources at the start of the winter, then making stopovers during bad weather or for refuelling or resting (especially amongst juveniles) is unlikely to have an adverse effect on future

fitness in geese, which have the luxury of being able to stage in terrestrial habitats. Indeed, heavier birds show reduced take-off ability (Witter *et al.* 1994; Metcalf & Ure 1995; Lind *et al.* 1999), which had led to the mass-dependent predation risk hypothesis (*i.e.* with heavier birds being more susceptible to predation, body mass should be lower during periods of enhanced predation risk; Bednekoff 1996). Hence, Brent Geese might be averse to fuelling up too much in autumn if there is a pay-off in terms of predation risk. On the other hand, Brent Geese may need some additional stores if they have to stop on the open ocean during bad weather, because of the risk of mortality (in both spring and autumn) on burning too much fuel if flying into head winds, or on being blown off course and missing landfall areas (*e.g.* Pennycuick *et al.* 1996, 1999). With no opportunity to refuel at terrestrial stopover sites, however, it is expected that Brent Geese are more likely also to adopt the time-minimiser migration strategy during autumn migration and we predict that the time taken to migrate in autumn would be similar to that in spring.

This study aims to use satellite telemetry to determine whether migration duration for Light-bellied Brent Geese in autumn differs from results of earlier research, which described the timing of their migration in spring (Clausen *et al.* 2003). Recent reviews have demonstrated that birds tagged with backpack-mounted transmitters and other tracking devices may, to some extent, be adversely affected by these devices (*e.g.* Bodey *et al.* 2018; Lameris *et al.* 2018; Clausen *et al.* 2020), with Lameris

& Kleyheeg (2017) calling for better reporting on such issues. The extent to which our tracked birds migrated at the same time as other, untagged individuals, therefore was also assessed.

Materials and methods

Geese were caught using cannon nets at Mågerodde on the island of Mors, Denmark (56°47'N, 8°33'E), on 16 May 2001 and 27 April 2011, and at Boddum Peninsula in Thy, Denmark (56°42'N, 8°31'E), on 3 May 2011. In total, 110 Brent Geese were marked individually with a combination of uniquely coded plastic leg rings and with numbered metal rings. Sixteen satellite transmitters from Microwave Telemetry were attached to geese: seven 30 g battery-powered Platform Transmitter Terminals (PTT) with Doppler technology in 2001, and nine 30 g solar GPS PTTs from 2011. The PTTs were fitted to the back by clipping a small number of back feathers with scissors to expose an area about half the size of the transmitter base. We then used Loctite superglue to attach the transmitter to the down feathers on the bird's back (just behind and intermediate between the shoulders), and the transmitter was additionally held in place by a knicker elastic harness which crossed on the sternum (after Glahder *et al.* 1998). To avoid potentially adverse effects of transmitter attachment on female breeding success (*cf.* Ward & Flint 1995), only males were tagged with transmitters.

After release, geese in the 2001 transmitter group (birds E–K) were tracked via the Argos satellite system using Doppler technology (Clausen *et al.* 2003) and those in the 2011 transmitter group (birds M–S) were

followed using a combined uplink of GPS positions via the satellites and Doppler. In 2001, the PTTs were programmed to transmit continuously from 19 August–30 September, and although batteries were partially depleted in early September, the performance of all transmitters improved when birds embarked on migratory flights (when solar panels were fully exposed and batteries recharged). On the specific days when the birds E–K (except J) migrated (see Table 1) an average of 10.1 positions were collected per day (range: 5–15), and migratory tracks were described from an average of 50 positions (range: 23–89). In 2011, the transmitters were programmed to collect 11 GPS positions per day (at 2 h intervals from 03:00–23:00 h) from 1 August–30 September, and to submit data every third day, when Doppler locations also became available. In 2011, all batteries were depleted when the birds started migrating, and the transmitter only became active after some hours of flight, after which time solar power was sufficient to recharge the battery on migration. For this reason, none of the 2011 birds provided complete autumn tracks, but we present these data to show the direct flight in the later stages of their migration. On migration days, the transmitters collected an average of 8 GPS positions (range: 2–12 for six birds, with one transmitter also occasionally recording a position at 02:00 h), and 11 Doppler positions (range: 4–23 for five birds, the sixth bird having migrated on days between uplinks to the satellites, so provided no Doppler data).

The quality of the location data ranged from Doppler B (least precise), through Doppler A, 0, 1 and 2, to the Doppler 3 and GPS (G) (most precise) positions. In order to compare directly between spring and autumn migration, data selection and analysis followed the earlier protocols from spring 2001, which are fully and comprehensively described in Clausen *et al.* (2003). The autumn migration routes were mapped by incorporating the location data into ArcGIS v. 10.1, using coordinates that indicated the beginning and end of the migration (from *c.* 76°–55.6° longitude). In line with the spring 2001 protocols, autumn 2011 low quality data (positions 0, A, B) were only accepted when flight speeds between adjacent positions were < 120 km/h. In 2011, all low quality data (positions A, B) were rejected unless they covered a gap of > 1 h in the transmission interval, and data classed as 0 were only accepted when flight speeds between adjacent positions did not exceed 120 km/h. This rejection protocol from Clausen *et al.* (2003), applied to secure comparisons between years, was supported by the absence of GPS-based travel speeds of > 120 km/h in 2011.

As with the spring 2001 data (Clausen *et al.* 2003), minimum speed (summed orthodrome distance between locations, divided by duration), maximum speed (summed loxodrome distance between locations, divided by duration) and their averages were calculated between adjacent positions for all birds tracked during autumn migration, using the formulae of Imboden & Imboden (1972). On inspecting the satellite telemetry data, individual stops (of < 48 h, to differentiate them from "stopovers" as defined by Kölzsche *et al.*

Table 1. Autumn migrations, including the number of stops, for individual Light-bellied Brent Geese tracked using satellite telemetry, from 7–24 September 2001 (Birds E–K) and from 18–24 September 2011 (Birds M, O-S).

Bird ID and year	Departure date	End date	Total distance (km)	Optimal[2] orthodrome distance (km)	Difference from optimal direct route (%)	Duration (h)	Average speed (km/h)[3]	Max speed (km/h)[4]	Min speed (km/h)[4]	Number of stops[1]	Average stop duration (h)[1]
E 2001	17 Sept	20 Sept	2,624	2,453	6.5	76.5	34	89	16	1	13.7
F 2001	9 Sept	13 Sept	2,786	2,464	11.5	92.8	30	99	15	2	11.8
G 2001	19 Sept	24 Sept	2,695	2,478	8.0	64.1	42	108	38	0	0.0
H 2001	7 Sept	9 Sept	2,500	2,442	2.3	46.7	54	117	23	0	0.0
I 2001	17 Sept	–	634	570	10.0	23.7	27	95	14	2	2.7
J 2001	19 Sept	23 Sept	2,899	2,644	8.8	91.3	32	120	12	2	9.2
K 2001	16 Sept	21 Sept	2,609	2,416	7.4	107.3	24	104	12	6	7.4
M 2011	–	–	1,895	1,682	11.3	87.1	22	97	10	2	20.2
O 2011	–	18 Sept	985	964	2.1	19.2	51	144	43	1	1.0
P 2011	–	15 Sept	1,191	896	24.8	25.0	48	76	19	1	2.0
Q 2011	–	18 Sept	1,906	1,713	10.1	37.0	52	141	10	1	1.7
R 2011	–	15 Sept	1,574	966	38.7	33.0	48	87	11	4	2.0
S 2011	–	24 Sept	533	451	15.4	239.6	2	25	10	2	117.8
Mean ± s.d.	–	–	2,685 ± 141*	–	12 ± 9.8	80 ± 22*	36 ± 15	100 ± 30	18 ± 11	–	–

[1]Stops were defined as periods where migration speed was < 20 km/h for > 1 hour. No stops were of > 48 h, which would qualify as stopovers *sensu* Kölzsche *et al.* (2016). [2]The optimal orthodrome migration indicates the shortest distance between the location recorded on Svalbard immediately prior to migration and the arrival point at the staging or winter area, or the last position recorded. [3]The average speed is the total travelled distance divided by the total duration of the migration, including stops. [4]Maximum and minimum speeds in 2001 and 2011 are both calculated on the basis of two successive positions along the migration. *Includes only those birds that were tracked successfully throughout migration (birds E, F, G, H, J and K).

2016) were classified as possible refuelling and resting periods when migration speeds of < 20 km/h were sustained for > 1 hour. Calculation of average migration distance and duration was based exclusively on 2001 data, because the early parts of the route were not recorded in 2011 due to battery depletion as day-length shortened in the arctic. The mean distance of the spring migration was calculated as the mean of the shortest (summed orthodromes) and longest (summed loxodromes) estimated tracks in Clausen *et al.* (2003). A two-tailed *t*-test with two-sample equal variance was used for statistical comparisons of spring and autumn migration distances.

In order to compare the migration timing of tagged birds with those of unmarked individuals, we downloaded observations of migrating Light-bellied Brent Geese from the citizen science portals of three major Nordic BirdLife partners: for Norway (www.artsobservasjoner.no), Denmark (www.DOFbasen.dk) and Sweden (www.artportalen.se). To minimise double-counting, data obtained for autumns 2001 and 2011 were inspected carefully for obvious duplicates (*i.e.* multiple observers reporting similarly sized flocks from the same or nearby sites on the same dates), and only the largest daily total was used in the analysis (see Vissing 2012 for full details). The dataset was dominated by observations from a few observation sites. These were: 1) a few sites in southwest Norway (*e.g.* Stad and Lista, where flocks from the former might fly both to Lindisfarne or Denmark, whereas the latter are most likely destined for Denmark); 2) two sites in Denmark (Blåvandshuk and Skagen, where birds at the

former site are on migration to the Wadden Sea, the southernmost wintering site in Denmark (Clausen & Fischer 1994), while birds at the latter are arriving to more north-easterly locations in Denmark); and 3) Hönö in western Sweden (where flocks on southbound migration are likely to have been wind-blown into the Skagerrak, on migration towards eastern Danish wintering sites).

Results

Tagged Brent Geese departed from Svalbard between 7–19 September and arrived in Lindisfarne during 9–24 September. In 2001, they covered on average 2,685 km (s.d. ± 141 km) in 80 ± 22 h (Table 1) during autumn migration, which did not differ significantly from the 2,526 ± 117 km covered in 77 ± 40 h during spring migration (tabulated in Clausen *et al.* 2003) ($t_{1,11}$ = –0.14, P = 0.89, n.s.). The distance actually travelled in autumn was on average 12 ± 9.8% longer than the optimal direct orthodrome route. On combining the 2001 and 2011 data, the Brent Geese were found to migrate at an average speed of 36 ± 15 km/h (including stops) during autumn, and reached average maximum and minimum speeds of 100 ± 30 km/h and 18 ± 11 km/h, respectively (Table 1).

Prior to autumn migration, the Brent Geese seemed to move south within Svalbard (Denny *et al.* 2004) and departed from Sørkapp Landet (76°39'N, 16°40'E) or Sørkappøya (76°28'N, 16°46'E) heading towards the west coast of Norway. Birds G and H made non-stop migrations and the rest made 1–6 stops (mean ± s.d. = 1.8 ± 1.63; Fig. 1b, 2b, Table 1), mostly offshore or in shallow water, presumably to rest. Only M
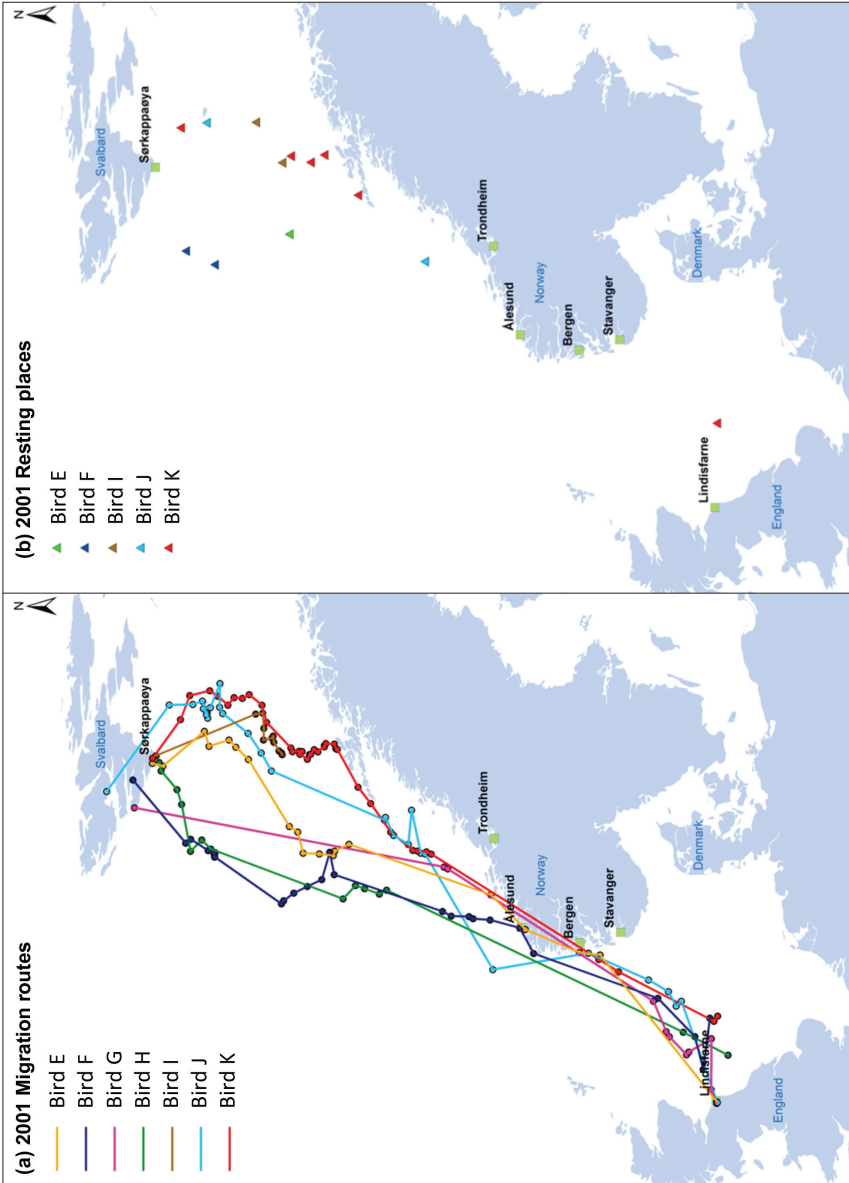
Figure 1. Autumn migration routes of Light-bellied Brent Geese tracked using satellite telemetry in 2001, showing complete migration routes (left) and resting areas (right). Each colour represents a different individual goose. The Brent Geese rested only on open water, in the Barents Sea and/or the Norwegian Sea (birds E, F and I, recorded until signal loss) and K rested on the North Sea. Birds G and H migrated non-stop from around Sørkappøya to areas around Lindisfarne.

and S rested on terrestrial habitats, with bird M having a single terrestrial stop apparently at or close to a small island, whereas bird S made terrestrial, shallow water and off-shore stops along the Norwegian coast starting at around Trondheim, before the signal was lost due to battery depletion near Bergen. In analysing the number of stops, the lack of data from the earliest half of the transmission period in 2011 due to battery depletion restricted our ability to conclude much about the total flight distance for that year.

The autumn migration included two open sea crossings. Tagged Brent Geese flew first from Sørkapp Landet and Sørkappøya in Svalbard, crossing the Barents Sea and parts of the Norwegian Sea to the west coast of Norway, which they reached at different places; *e.g.* near Andøya (69°20'N, 15°49'E), Røst (67°25'N, 11°52'E), Smøla (63°33'N, 7°44'E) or Ålesund (62°28'N, 6°08'E). From there they continued along the coast, primarily over sea but relatively close to the coastline, before heading across open water over the North Sea to Lindisfarne. Birds left the Norwegian coast from Ålesund or Stavanger (Fig. 1, Fig. 2).

Data from the citizen science portals indicated that the timing of autumn migration differed markedly between the two years. Birds counted on migration in southern Norway, western Sweden and northern Denmark (most likely on the day before or during the arrival day) arrived in a bimodal pattern in 2001, with an early wave between 5–10 September, and a second between 20–25 September (Fig. 3). Two of the tagged birds migrated with the first, and four with the second waves (Table 1, Fig. 3).

In 2011, mass migration took place between 10–15 September, and the remaining birds arrived gradually thereafter (Fig. 3). On this occasion two tagged birds arrived during the mass migration, two immediately thereafter, and another arrived slightly later (Table 1, Fig. 3). Hence, none of the tagged birds showed obviously delays in their migration timing relative to the rest of the population.

Discussion

The 2001 tracking data confirmed the lack of a difference in the time taken by Light-bellied Brent Geese breeding on Svalbard to complete their spring and autumn migrations. Our previous study found that they conduct rapid, almost non-stop migration in spring (77 ± 40 h), taking only a few stops (mean ± s.d. = 3.3 ± 3.95, range = 1–11) of 4.0–24.0 h (Clausen *et al.* 2003). Here we describe very similar behaviour for the birds' autumn migration; two Brent Geese travelled non-stop to their wintering areas, and the rest made very few (1–6) stops (see Table 1), of differing durations (1.0–20.0 h) and generally all in off-shore habitats entirely unsuitable for foraging. One exception was bird M, which appeared to make a single terrestrial stop on or close to a small island. As in spring, with a lack of suitable refuelling places, the tagged Brent Geese completed their autumn migration promptly (80 ± 22 h). Bird S was omitted from this analysis, because it showed different migratory behaviour, with many small near-coastal stops. It had not completed its migration when contact with the transmitter was permanently lost.

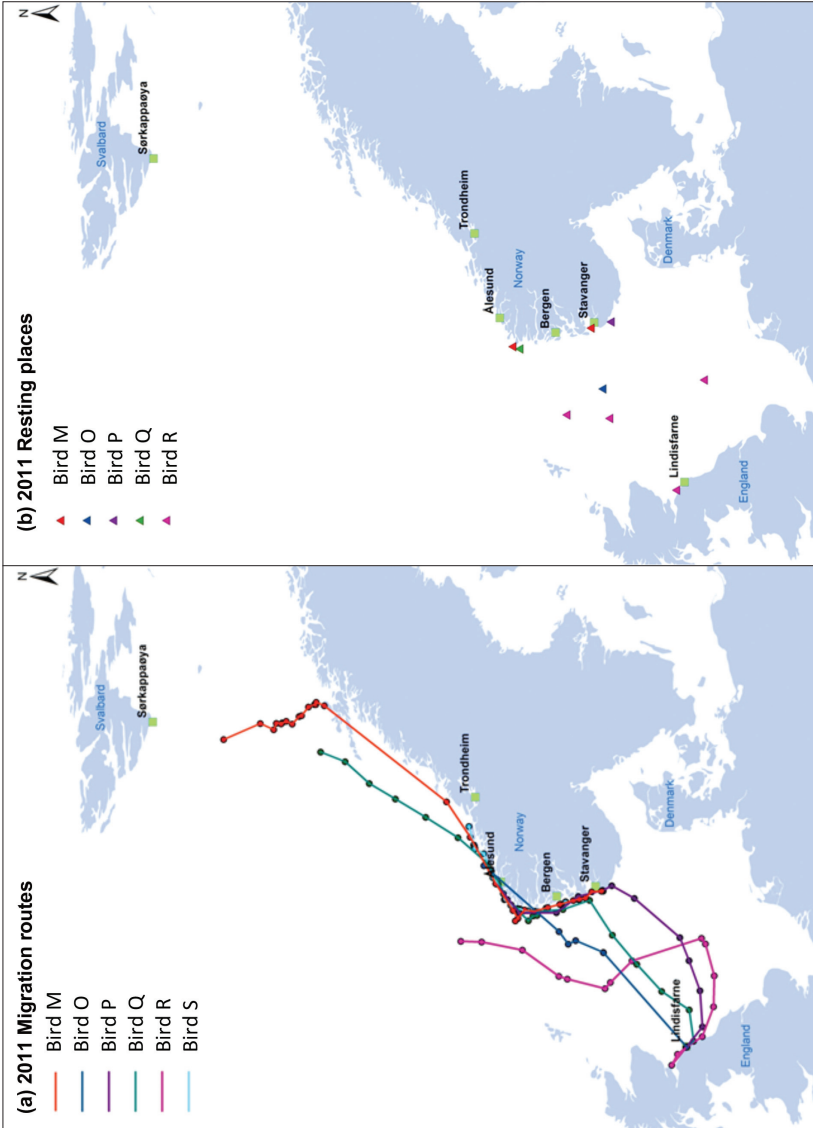Given that the timing of migration for all tagged birds, both in spring (Clausen *et al.*

Figure 2. Autumn migration routes of Light-bellied Brent Geese tracked using satellite telemetry in 2011 showing complete migration routes (left) and resting areas (right). Each colour represents a different individual goose. Due to battery depletion, data for some parts of the migration route (*i.e.* on traversing the Barents Sea) were lacking. Further south, the Brent Geese rested primarily on open water in the Norwegian and North Seas (birds M, O, P, Q and R). Bird M had a single terrestrial stop. Bird S migrated slowly along the coast, taking rests both at terrestrial sites and on the open sea. Resting sites used by bird S are not illustrated in the resting map (right), as these positions were similar to the transmission points at the route map (left).
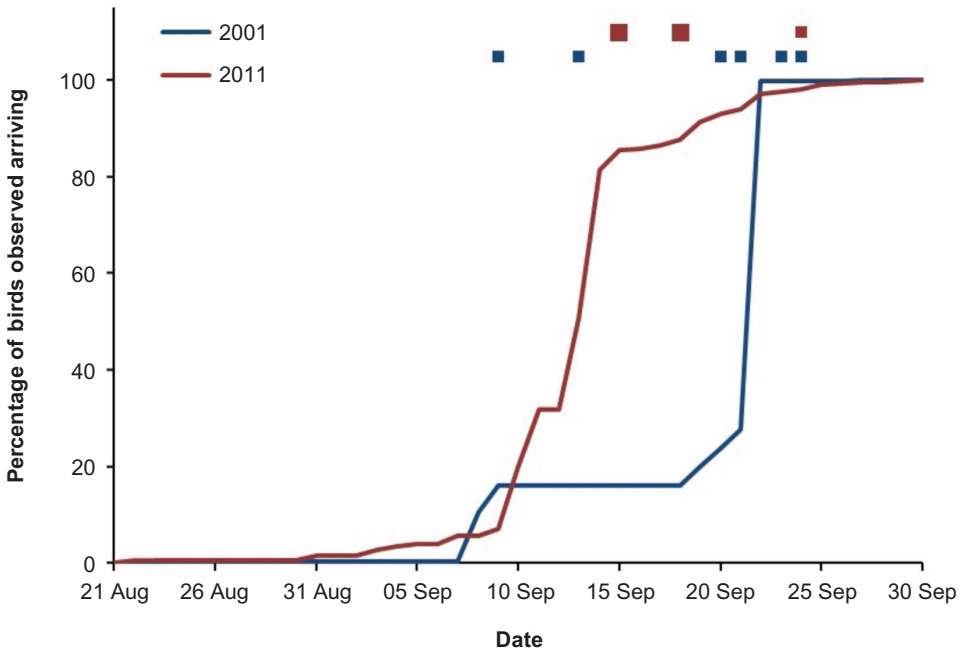
Figure 3. Cumulative proportions of Light-bellied Brent Geese counted on southbound migration in southern Norway, western Sweden and Denmark during autumns 2001 (*n* = 1,033 birds) and 2011 (4,211 birds). Small squares show when birds with satellite transmitters arrived (from Table 1), with the larger squares representing two individuals each.

2003) and autumn (this paper), coincided with main migratory waves observed for thousands of non-tagged individuals, we believe that the migratory flight behaviour and speeds of the birds presented here may be representative of the majority of the population. Interestingly, all tagged geese flew directly to the autumn staging site at Lindisfarne, when 4,200 birds had arrived in Denmark by early October 2011 (Pihl *et al.* 2013), and only 3,100 birds had reached Lindisfarne at the same time (Andrew Craggs, Lindisfarne National Nature Reserve, pers. comm.). Hence, the birds tracked during our study (caught during spring staging in western Limfjord,

Denmark) apparently all followed different migratory patterns to the thousands of geese which stage in the eastern Limfjord and other sites in northeast Denmark during spring and autumn migration.

In contrast to the non-stop flights undertaken by Light-bellied Brent Geese, the Dark-bellied Brent Geese *Branta bernicla bernicla* which breed on the Taymyr Peninsula in arctic Russia and winter on the Wadden Sea make several refuelling stopovers during spring and autumn migration, each lasting for > 48 h (Green *et al.* 2002). The 5,004 km migration of the Dark-bellied Brent Geese (Green *et al.* 2002) is almost twice that of the Light-bellied

Brent Geese; hence their need for more frequent refuelling. Instead of flying the shortest orthodrome route over the Fennoscandinavian taiga and mountains then continuing across the Arctic Ocean to Siberia, the Dark-bellied Brents choose to fly along the Baltic Sea and White Sea coastlines (increasing the distance of their journey by 16%), presumably because of the advantage gained from proximity to feeding, drinking and sheltered resting places if required. Following the coast also has navigation advantages, especially in poor visibility. Clearly, Light-bellied Brent Geese are energetically capable of flying at least 2,700 km without stopping, as illustrated by the results presented here and also those from the previous spring tracking studies. Previous theoretical modelling, however, suggested that females undertaking a prolonged flight of > 2,700 km in spring would have difficulty in both completing migration and laying a clutch of eggs without substantial additional energy from supplementary feeding (Clausen *et al*. 2003), so it seems that they are close to the limit of being able to do so under their current migration strategy.

Following the long-distance non-stop flight, the fat stores accumulated by Light-bellied Brent Geese to fuel migration are likely to be heavily depleted by the time that the birds arrive at their autumn staging and wintering sites. Data from shot birds (collected by Fog 1967), indicate early autumn body masses of *c*. 1,305 g (Clausen *et al*. 2012), compared with for instance *c*. 1,860 g for males and *c*. 1,780 g for females caught at spring staging sites (Clausen *et al*. 2003). The ability of geese to survive the

winter is enhanced by their accumulation body reserves in autumn, which are utilised during periods of shorter day-length and low temperatures in mid to late winter, when food intake may fail to meet daily energetic expenditure (*e.g.* Owen *et al*. 1992; Butler *et al*. 1998; Wang *et al*. 2013). For this reason, it might be crucial for individuals to arrive on the autumn staging grounds when the food resources are of highest energetic quality and quantity. Brent Geese have a strong preference for coastal habitats where eelgrasses *Zostera* sp. and Sea Lettuce *Ulva lactuca* are abundant, and they use these before switching to feed at terrestrial sites, most likely because *Zostera* in particular is energetically superior to vegetation available in other habitats suitable for the geese (Inger *et al*. 2008; Clausen *et al*. 2012, 2013). The *Zostera* and *Ulva* food resources for Brent Geese at coastal sites therefore are the first to become depleted during the autumn, whereupon they move on to nutritionally less attractive terrestrial alternatives such as saltmarshes and cereal fields (see Clausen *et al*. 2012). Early arrival in autumn therefore might serve to maximise post-migration fattening and contribute to improved winter survival, which could enhance survival of early migrants and select for migrating from the breeding areas at a particular time.

Alternatively, the rapid non-stop migration undertaken by the geese could simply reflect the current lack of their preferred *Zostera* beds along the migration route. Larger *Zostera* beds suitable for foraging are highly restricted along the Norwegian north and west coasts, and those that do exist occur in water depths most likely too deep for the geese to access

(Bekkby *et al.* 2008; Jørgensen & Bekkby 2013). The largest known *Zostera* bed in northern Norway only covers 0.324 km² (Jørgensen & Bekkby 2013). In contrast the large and easily accessible Dwarf Eelgrass *Zostera noltii* and Narrow-leaved Eelgrass *Zostera angustifolia* beds in Lindisfarne covered 7.6 km² in 1989–1992 (Clausen & Percival 1998) and 5.9 km² in 2013 (Ahmed 2015). Likewise, more than 4.6 km² of Common Eelgrass *Zostera marina* was found in the most important Danish autumn staging site of Nibe-Gjøl-Egholm in 2001, a year with very poor densities of *Z. marina* (Balsby *et al.* 2017; Clausen *et al.* 2017). Since then, *Zostera* densities have improved (Balsby *et al.* 2017) and the area covered expanded to ≥ 25 km² during 2012–2016 (Ørberg *et al.* 2018). Given the lack of suitable foraging sites along the Norwegian coast, and that tagged birds most often stopped at deep-water offshore locations (*cf.* Figs. 1 & 2, *i.e.* in places where they would not be exploiting suitable feeding habitats), suggests that these were most likely brief rests rather than stopover periods, perhaps induced by unfavourable weather conditions or by the birds needing to rest or drink, rather than to refuel. The present and perhaps also a historical absence of *Zostera* foraging areas along the migration route therefore might have shaped the non-stop migration we currently witness in Light-bellied Brent Geese.

Although the autumn and spring migrations seem to be undertaken by all individuals in just one stage, the two seasons differ quite markedly in the overall duration of their migration periods. In spring, all birds migrate in one or two waves and

within a very short time-frame of < 10 days (Clausen & Bustnes 1998; Clausen *et al.* 2003), whereas in autumn first birds arrive in late August and migration continues until the end of September or even early October (Clausen & Fischer 1994). The factors triggering departure of the Light-bellied Brent Geese in spring is most likely favourable tail-winds, as also found for the Dark-bellied Brent Geese (Ebbinge 1989), but those triggering autumn migration are poorly understood and should form the focus for future research. It is interesting that all of the tagged birds migrated directly to Lindisfarne, despite the fact that *c.* 60% of the entire population autumn stage and winter in Denmark. This anomaly calls for more telemetry studies of birds tagged from several spring staging areas to differentiate between geese of different breeding, staging and wintering provenance. On-board accelerometry devices would provide further simultaneous information on goose activity, to confirm individual behaviour during their stops (*e.g.* Weegman *et al.* 2017; Doktor *et al.* 2018).

Overall, despite the lack of time limitation in autumn, Brent Geese choose to complete their autumn migration in one leap. Late summer food availability in the high arctic is unlikely to be limiting, especially at low goose population densities, with both green graminoid growth and lipid-rich plant seeds continuing to provide a food resource for the geese. Thus Brent Geese may be able to attain optimal fuel stores immediately prior to autumn migration, reducing any need for refuelling en route. The ability to accumulate sufficient energy stores for long-distance non-stop

migration, prior to departure from the summering grounds, has also been recorded for some high arctic-nesting Far East Asian waterbirds, which do not migrate across oceans but the seemingly equally inhospitable habitat of the taiga forest biome (Wang *et al.* 2018).

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Photograph: Light-bellied Brent Goose ringed "white DY" on the shore of the Boddum catch site in May 2011, by Kevin K. Clausen. It is one of 120 individual birds ringed at Lindisfarne during 1991–1998 and resighted at Boddum during 1991–2011, highlighting the importance of the former as a wintering site and the latter as a spring staging area for these birds.