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Migration routes, stopover sites and home range sizes of Taiga Bean Geese (Anser fabalis fabalis) breeding in northern Sweden and central Norway tracked by GPS tags

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Abstract

The Taiga Bean Goose (*Anser fabalis fabalis*) has shown a recent decrease in population size. For geese breeding in central Scandinavia, the delineation between different subpopulations is not entirely clear and more detailed knowledge regarding migratory routes is still lacking.

Moulting Taiga Bean Geese caught at Vilhelmina, Sweden were equipped with solar-powered GPS satellite transmitters. In this study the route, timing and stopover use was determined for autumn and spring migration. For several major sites the home range was also determined as well as the similarity in space use within and between years for every goose. A total of 13 tagged Taiga Bean Geese eventually provided (partial) telemetry data for three years.

Two distinct routes were revealed. The majority flew to Töreboda to stage during spring, before flying to their breeding grounds in southern Västerbotten County, Sweden. Two geese however migrated along the Swedish-Norwegian border to breed in Børgefjell national park, Norway. During autumn all birds departing from northern Sweden used a long duration stopover at Töreboda before returning to their wintering grounds in Thisted, Denmark. Their autumn migration varied from 11 to 150 days. In contrast, the two Norwegian breeding birds flew straight to their destination in Thisted, generally completing their autumn journey within less than a day. Both groups displayed high fidelity and return rates to their wintering and major stopover sites. Although the data of this study only includes two birds breeding in Norway, the consistently distinct migratory route and behaviour, combined with recent genetic data, indicates that these birds are largely distinct from their Swedish counterparts. Uncovering discrete migratory routes is thus crucial for implementing more targeted conservation efforts towards more vulnerable subpopulations. Encompassing 3 years of telemetry data, this study contributes towards a first step in better understanding the delineation and connectivity of flyways of Taiga Bean Geese breeding in Scandinavia.

Keywords: Taiga Bean Goose, Anser fabalis fabalis, migration, gps, stopovers, home range

Contents

1 Introduction

For a migratory species it is crucial to understand where they travel to and which sites they use during different times of the annual cycle. When a species uses flyways which are largely distinct, this can have important implications for management. The Bean Goose (*Anser fabalis*) in the Western Palearctic consists of two subspecies which both have a distinct geographical range, *A.f. fabalis* and *A.f. rossicus*, or Taiga and Tundra Bean Goose respectively (Nilsson et al., 1999; van den Bergh et al., 1999). Like many Goose species, the Tundra Bean Goose has seen a recent increase in their population size (Fox et al., 2005). The Taiga Bean Goose however is currently one of the few Goose species with a declining population trend (Mooij, 2011). The population size of Taiga Bean Geese has gone from an estimated 100.000 individuals during the 1990s (Fox and Madsen, 1999) to 63.000 in 2015 (Marjakangas et al., 2015). Recently, the AEWA (Agreement on the Conservation of African-Eurasian Migratory Waterbirds) released an action plan specifically aimed at the Taiga Bean Goose (Marjakangas et al., 2015) as a conservation effort. The ISSAP (International Single Species Action Plan) recognises the existence of several distinct flyways. Stable isotope analysis of flight feathers has also further supported the proposition that these flyways are largely discreet (Fox et al., 2017). For Taiga Bean Geese breeding in Europe two separate flyways are recognised. The Central Flyway Unit (CFU) encompasses a breeding habitat covering northern Fennoscandia (as well as adjacent parts of Russia), while those breeding in north and central Sweden and central and southern Norway fall under the Western Flyway Unit (WFU). Generally, Taiga Bean Geese following the CFU are thought to migrate to their breeding grounds in northern Fennoscandia and Russia along the Baltic Sea and Gulf of Bothnia, while those flying along the WFU pursue a route more inland through Sweden and the Scandinavian mountain range (for more details see Marjakangas et al., 2015. p.12 figure 2.). For these flyways the estimated population sizes based on winter counts are approximately 1500 for the WFU and 35.000 individuals for the CFU in 2014.

For the WFU several fragmented breeding subpopulations are also thought to exist with for instance a population breeding in southern Västerbotten in Sweden (Marjakangas et al., 2015), Dalarna in central Sweden (Mitchell et al., 2016) and a modest population in central Norway (Kroglund and Østnes, 2016). A study of GPS tagged Taiga Bean Geese wintering in Scotland suggested that these birds have largely discrete migration routes and wintering sites (Mitchell et al., 2016). A recent study by De Jong et al., 2018 analysed genetic material taken from Taiga Bean Geese at moulting sites Vilhelmina, Sweden and found that at least two subpopulations were present, each genetically distinct. However, the study also highlighted the need to combine these findings with more knowledge of geographic range and breeding range of these populations. Neckband efforts (e.g.: Nilsson and Pirkola, 1991; Pirkola and Kalinainen, 1984) have revealed the basic movements between key sites. A more detailed understanding however of the delineation of these flyways as well as possible subpopulations is still currently lacking. Recent tracking technology allows us to gain a more detailed insight into the movements undertaken by birds. For a migratory species, identifying key sites and how these form the "links in the chain" is paramount to their protection. It also provides an opportunity to detect important sites which might previously have gone unnoticed during their more elusive breeding and moulting periods. This study makes use of data provided by Taiga Bean Geese equipped with GPS-transmitters which were caught during moult in Vilhelmina, Sweden. The focus of this study is to provide insight into the movement patterns and key sites utilised by individually tagged Taiga Bean Goose. The main objectives will be to:

- investigate the possible occurrence of subpopulations with discrete breeding ranges.
- identifying key sites during the breeding, wintering and staging period
- determine the route and timing
- determine the stopover sites utilised during spring and autumn
- determine the home range size and home range size overlap for wintering and staging sites
- contrast these findings against other known (sub)populations in order to determine how discrete these birds are

2 Material & methods

2.1 Satellite telemetry

Individual Taiga Bean Goose were caught during mid-July at Vilhelmina, Sweden during their moulting period and were deployed with transmitters (n = 5 in 2014 and n = 16 in 2015). Birds were equipped with solar powered neckband-attached GPS loggers (Ecotone Telemetry, ~30g) which provided locations through means of SMS (short message service). Neck band collars were also marked with numbers for identification in the field. The number of locations received per day ranged from 2 to 48, depending on solar conditions and season. During winter season for instance, collars transmitted fewer locations per day. In a few cases transmitters gave several duplicate locations. When recordings were less than 20 minutes apart, the average location was selected, the duplicates removed and the time closest to the hour was retained. Positions with unrealistically high flight speed (>150km/h) were manually deleted from the dataset. By analysing the relocation from day to day I assumed that a period of at least 28 days (the incubation period) in which movement was consistently under <10km a day between May and July as well as the absence of a moult migration meant that the goose had made a nesting attempt. Sightings retrieved from http://www.geese.org were also used to confirm whether a goose was observed with offspring.

2.2 Data analysis

2.2.1 Migration

Spring migration was considered to start from the last position at the winter site and last until the arrival at the summer breeding grounds. Autumn migration was described as the movement geese made between their breeding/moulting ground and their wintering grounds. The total migration duration was calculated as the difference between departing from wintering up until arrival at the summer grounds (spring migration) or vice versa (autumn migration).

2.2.2 Stopover sites, travel distances and flight speed

A cluster of at least 2 positions were considered stopovers when speed between successive positions was less than 15 km/h. The average longitude and latitude of every position assigned to that particular stopover was used to calculate the location. A distinction was made between long and short-term stopovers. A stopover was considered long term when the duration of stay was at least 48 hours, approximately the time needed to refuel (van Wijk et al., 2012). Detours of less than 8 hours were assigned to that particular stopover. The term stopover will be used hereafter to refer to long duration stops, unless specifically stated otherwise.

The distance between stopovers was calculated by the great circle distance between them. Migratory movements between stopovers were considered for analysing flight speed when exceeding 15 km/h for successive positions. The amount of time spend on flight between a non-flight position and a flight position carries a high level of uncertainty. For calculating ground speed, I therefore excluded speed calculations between flight points and arrival or departure from stopovers. For all stopovers the duration of stay was also determined. I also checked for possible missing data. No arrival and departure points at stopovers which differed more than 12 hours between previous or subsequent points were found. I therefore did not exclude any of these stopover arrival or departure points.

2.2.3 Home range analysis and overlap

All frequently visited stopovers were used for calculating home range sizes. This included all those which were visited by more than one goose during multiple years as well as the wintering site. The home range analysis was performed starting from arrival until the departure of each individual goose. Two separate methods were used to calculate home ranges, minimum convex polygons (MCP) and Brownian bridge movement models (BBMM). To give an indication of site fidelity between years and shared space use amongst individuals I also calculated the proportion of overlap.

Minimum convex polygons

The smallest polygon drawn around a set of locations is called a MCP (fig.1). While the MCP method offers no interpretation of possible space-use within the home-range, it is the most commonly used home-range estimation method (Calenge, 2015). The MCP method was included to allow for robust comparisons amongst studies. An inclusion of either 95% or 100% of all points are the most widely used estimates (Laver and Kelly, 2008) and by comparing both the latter produced a better visual representation of the data. 100% MCPs were calculated using the adehabitatHR package (Calenge, 2006) and performed using R version 3.5.0 (R Core Team, 2018).

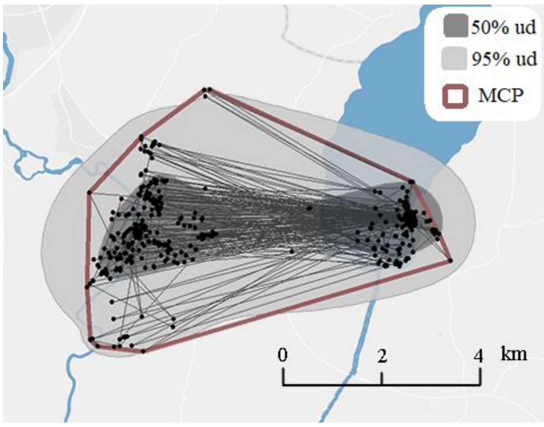

Figure 1: An example of a home range size of a goose at Töreboda during autumn 2016. MCP (24.9 km2) is represented by a brown line. The utilization distribution calculated by the BBMM is shown in light grey for 95% (32.5 km2) and dark grey for 50% ud (7.1 km2).

Brownian Bridge Movement Models

Contrary to MCP method, BBMMs also take into account the utilization distribution (UD), i.e. a probability distribution which gives the probability that an animal might be found at any given point at a certain location (Van Winkle, 1975). BBMMs are also considered a more appropriate method than kernel density estimates since it takes into account the time between successive locations when calculating the utilization distribution (Horne et al., 2007). The home range sizes were estimated for both 95% UD as well as for core use areas with 50% UD (fig.1) and implemented by the adehabitatHR package. Calculating utilization distribution using a BBMM also requires a smoothing parameter accounting for the imprecision of the relocations and a parameter related to the speed during two successive relocations. Personal testing of data provided by a stationary GPS tag provided a standard deviation of 15.15 m., which was used for the location error. The second parameter was extracted using the *liker* function (adehabitatHR).

Home range overlap

Stopovers selected for home range analysis were also included for calculating the proportion of overlap. For stopovers which were used by multiple birds during the same period, I calculated the proportion of overlap between each individual to assess the degree of similarity in spatial use. In order to quantify fidelity, it was not only determined whether a bird returned to a stopover in a subsequent year but also the proportion of overlap for this individual between years. Using the kerneloverlap feature (adehabitatHR package) an index was given for the proportion of overlap ranging from 0 (no overlap) to 1 (100% overlap). The method used was “VI” (volume of intersection index), as described by (Fieberg and Kochanny, 2005). The VI method provides an index for the mutual overlap between two utilization distributions.

3 Results

A total of 13 transmitters (appendix I) were eventually used for analysis since eight failed to provide enough data points for at least one entire seasonal movement between wintering and summer grounds either due to loss of signal (n=6) or mortality (n=2). Out of 13 transmitters used, eight provided three full autumn and two spring migration tracks from 2015 to 2017. Four loggers stopped transmitting, of which one only the collar was retrieved. One spring migration route was also excluded due to partially missing data (most likely due to low battery conditions). Individual transmitters yielded 1776 to 10482 GPS relocations (appendix I).

3.1 Migration routes, schedule and stopover use

The loggers revealed two distinct migration patterns, with two separate breeding areas. Two out of 13 tagged geese had a more western bound route along the Swedish-Norwegian border, while the remaining geese restricted their migratory routes flying inland through central Sweden and along the west coast of the Gulf of Bothnia (Figure 2). The latter had breeding grounds located in Västerbotten Country in northern Sweden while the more western bound birds spend their breeding period in Børgefjell national park in Norway.

3.1.1 Spring migration

Departure from wintering grounds took place during late February until mid-April. A general pattern was seen in the majority of birds. Arriving between late February and mid-March, geese frequently used a stopover area around Ymse and Östen Lake (on the border of Töreboda, Mariestad and Skövde municipality) Sweden. To simplify matters, this stopover will be referred to as Töreboda. Afterwards, tagged geese either continued straight to their breeding grounds, or used stopovers close by (on the border of Jämtland and Västerbotten county). Departure dates from Töreboda were less variable, between the 13th and 24th of April during both years. Töreboda proved to be an important stopover for the Swedish breeding birds (mean duration of stay: 43 ±14.1 and 43 ±9.0 for 2016 and 2017, respectively). Only tagged goose id slus06 skipped this stopover during both years, instead making several stopovers closer along the coast of the Gulf of Bothnia (figure 2, figure 3), as well as one individual (svan06) during 2017. Arrival time at the breeding grounds in Västerbotten County took place between mid-April and early May.

The two Norwegian bound geese however had a different route in comparison. Leaving Thisted, both arrived at a small lake within Åsnes municipality (Hedmark) in Norway simultaneously (mean duration of stay: 17 ±1.4 and 28 ±0.8 in 2016 and 2017 respectively) and remained here during most of April. Upon departure from Åsnes the two birds dispersed to stop either at Strömsund municipality (Sweden) or Lierne in Trøndelag (Norway) before arriving at Børgefjell during both years. Arrival at the breeding grounds in Børgefjell was also notably later than those arriving at Västerbotten.

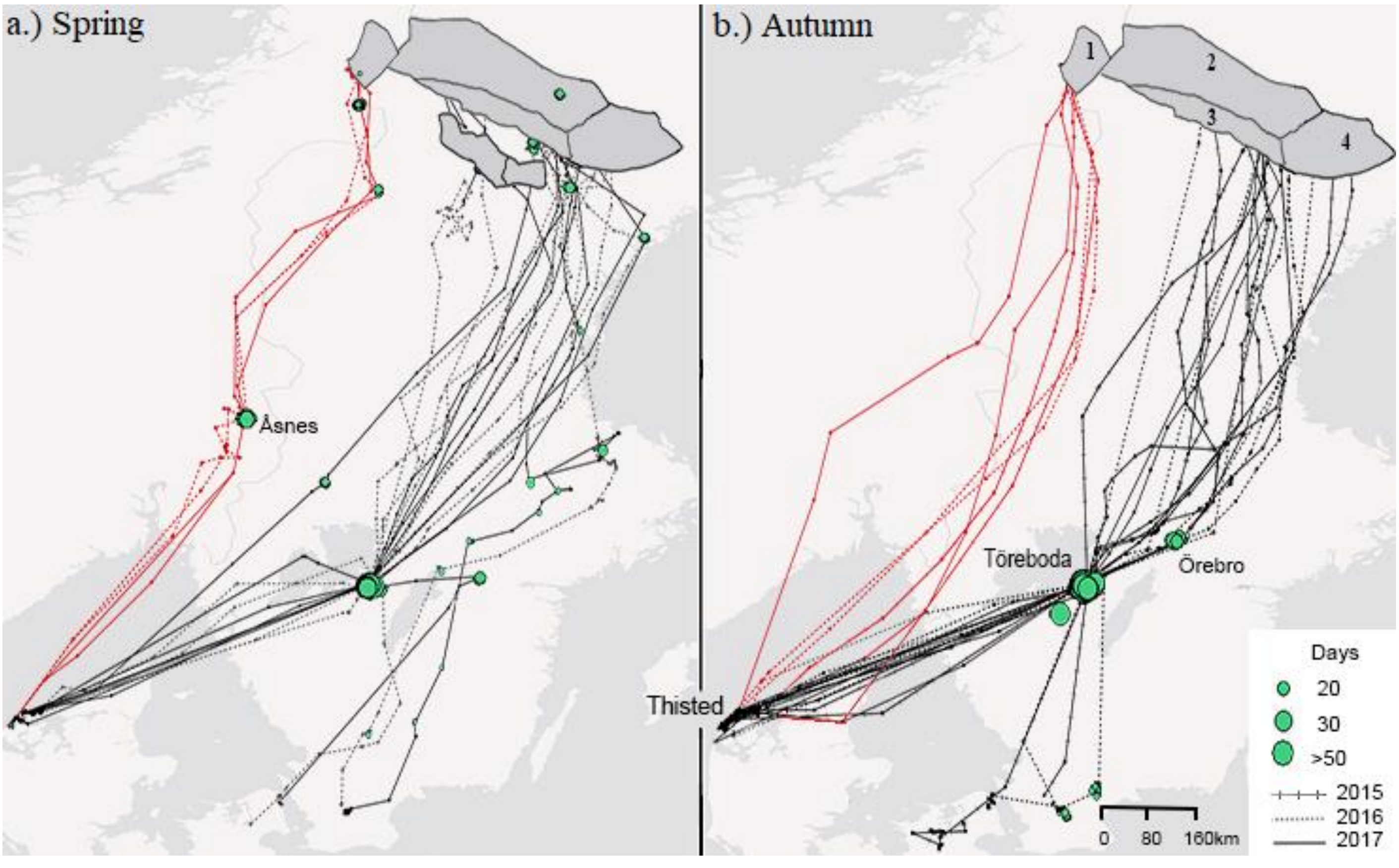

Figure 2. Migration route during a.) spring and b.) autumn. Routes in 2015, 2016 and 2017 are shown in crossed lines, dotted and straight lines respectively. Routes of tagged birds breeding in northern Sweden are shown in black, the two tagged geese (svan05 and svan07) breeding in central Norway are shown in red lines. 1 = Børgefjell national park, Norway, 2 = Vilhelmina kommun, Sweden, 3 = Dorotea kommun, SE and 4 = Åsele kommun, SE. Stopover (green circles) size is shown relative to length of stay.

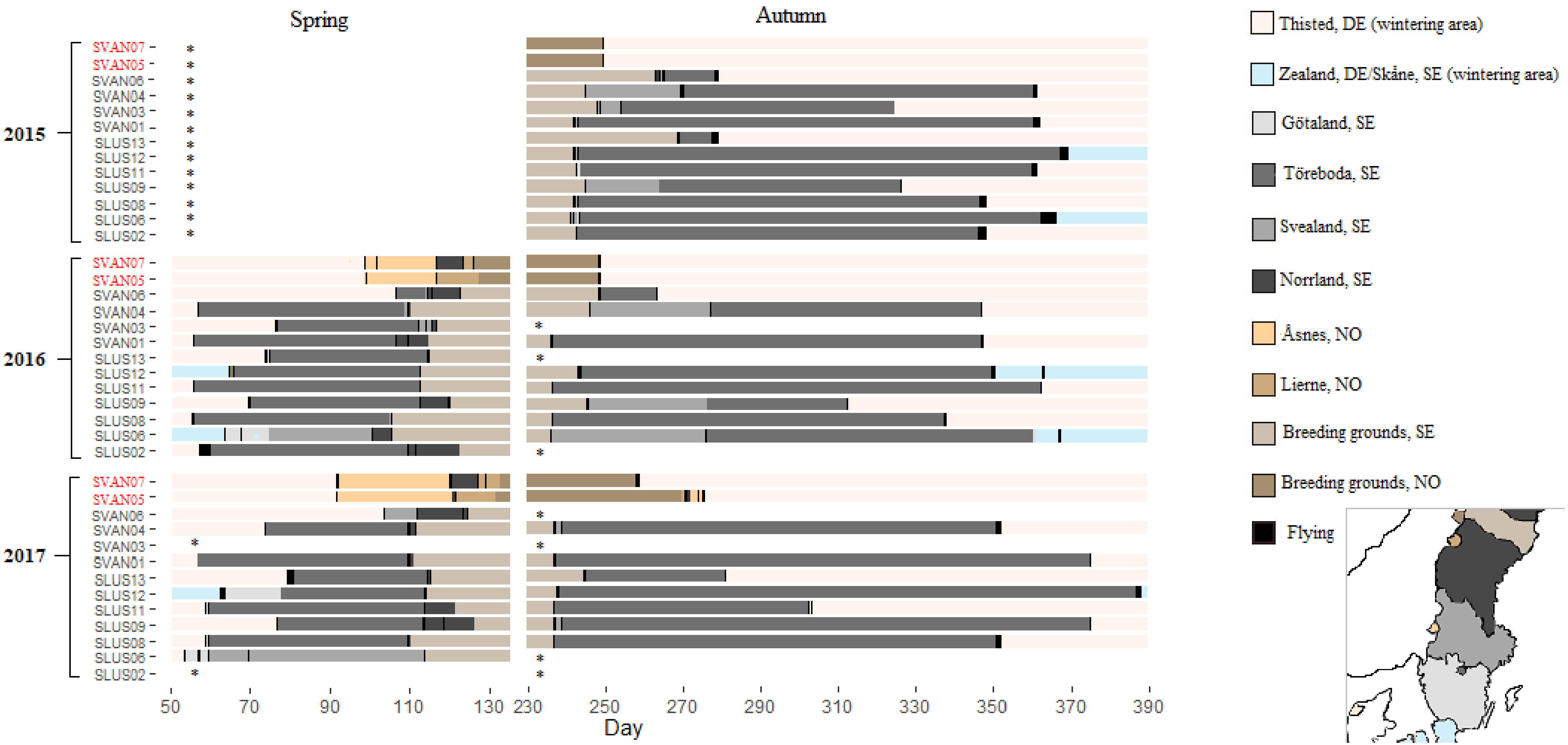

Figure 3. Spatiotemporal distribution of 13 collared Taiga Bean Geese, shown with the corresponding IDs from the transmitters. Movements to subsequent stopovers (both short and long term) are indicated by a period of flight (black). Colours of different locations are also shown in the corresponding map of Norway, Sweden and Denmark. Days are number of days counted starting from the 1st of January. Note that the two Norwegian breeding birds are id numbers svan05 and svan07, and are shown in red lettering. An asterisk (*) is shown when a logger had not yet started or had either ceased broadcasting.

During spring migration, birds made use of 1 to 6 stopovers (table 1). Total spring migration on average took 45 days (±15 and ±12 for 2016 and 2017 respectively) for all tagged geese during both years. Only the general breeding area is described in this study in order to protect the birds from any possible disturbance.

3.1.2 Autumn migration

During late August until early September most birds had left their breeding/moulting grounds. Autumn migration routes were comparable to spring migration. The geese breeding in northern Sweden displayed high fidelity (100%) to the stopover at Töreboda (mean duration of stay: 84 ±41.5, 81 ±38.6 and 107 ±41.6 days during 2015, 2016 and 2017 respectively). Before visiting Töreboda, tagged geese also occasionally arrived in Örebro municipality (3 out of 11 in 2015 and 3 out of 8 in 2016 but none in 2017), staying on average for 15 ±9.0 and 33 ±5.4 days in 2015 and 2016. Autumn migration for birds departing from northern Sweden varied from 11 to 150 days. In comparison, the Norwegian breeding birds generally reached their winter destination within less than a day during autumn, without making use of any stopovers.

3.2 Winter and summer grounds

Most Taiga Bean Geese (11 out of 13) resided in Thisted during the winter period (Figure 3). All tagged geese wintering in Thisted also consistently returned during the next two years. One goose however (slus06) spend both winters in Skåne County, and another (slus12) resided in both Skåne and Zealand, Denmark. Time spend by Taiga Bean Geese at their wintering grounds was highly variable lasting from 49 to 213 days (mean: 111 ±62, 115 ±62, 120 ±57 in 2015, 2016 and 2017 respectively. During the summer period, analysis of the loggers had revealed that several geese had made nesting attempts or raised offspring (appendix I). Those who did not make any nesting attempts had undergone a moult migration of 26 to 115 km, but stayed within Västerbotten County. Even though the two tagged birds breeding in Norway had spent their breeding period at a separate location, they spend their moulting period at Vilhelmina municipality, meaning their moulting site overlapped with several of the Swedish breeding birds.

Table 1: Summary of spring and autumn migration of Taiga Bean Geese breeding in northern Sweden and middle Norway. Shown are the departure and arrival dates, duration of migration, number of stopovers, duration spend at stopovers, distance between stopovers and speed during autumn (2015-2017) and spring (2016-2017) migration. Medians are accompanied by the range and averages are shown with the standard deviation (sd).

	Sweden					Norway				
	Autumn			Spring		Autumn			Spring	
	2015	2016	2017	2016	2017	2015	2016	2017	2016	2017
n	11	8	7	11	9	2	2	2	2	2
Median departure date	30-Aug	26-Aug	25-Aug	3-Mar	3-Mar	6-Sep	4-Sep	21 Sep	7 Apr	1-Apr
range	29 Aug-26 Sep	23 Aug-4 Sep	25 Aug – 1 Sep	23 Feb-15 Apr	21 Feb-13 Apr	-	-	15 Sep – 27 Sep	-	-
Median arrival date	14-Dec	12-Dec	18 Dec	23-Apr	23-Apr	7-Sep	5-Sep	24 Sep	5 May	11-May
range	6 Oct-4 Jan	20 Sep-2 Jan	8 Oct – 23 Jan	14 Apr-1 May	19 Apr-6 May	-	-	16 Sep – 3 Oct	4 May-6 May	11 May-12 May
Average duration of total migration (days)	92	97	109	48	48	<1	<1	3	28	41
sd	±41.9	±38.5	±41.9	±13.6	±13.1	±0.1	±<0.1	±2.9	±0.9	±0.9
Median nr of stopovers (short and long term)	3	2	1	4	4	0	0	3	6	6
range	1-5	1-6	1-2	1-6	2-5	-	-	1-4	4-7	3-8
Median nr of stopovers (>48 h)	1	2	1	1	2	0	0	0	3	3
range	1-2	1-3	1	1-4	1-6	-	-	-	2-3	2-3
Average time (days) spend at stopovers (>48 h)	27	38	75	13	13	0	0	0	5	7
range	<1-124	<1-125	<1-148	<1-57	<1-54	-	-	-	<1-17	<1-29
Average distance (km) between stopovers (>48h)	562	485	630	533	520	1051	1056	1062	363	313
sd	±171.6	±224.0	±106.6	±194.9	±195.9	±25.7	±0.11	±4.1	±221.1	±237.3
Average speed (km/h)	55	58	63	57	58	90	90	55	58	55
sd	±11.7	±15.5	±9.9	±17.0	±13.2	±25.0	±6.6	18.7	±15.5	±17.1

3.3 Home range size and overlap

The home range size was calculated for four stopover locations: Töreboda, Örebro, Åsnes and the winter area in Thisted (table 2). All four locations were visited during multiple years by more than one individual during the same period. Töreboda (spring and autumn) and Örebro (autumn) were visited exclusively by the Swedish breeding birds, while Åsnes (spring) was visited only by the two geese breeding in Norway. Both groups stayed in Thisted during the winter period. Home ranges calculated by BBMM (95%) for the Norwegian breeding birds separately mostly fell within the range of all geese recorded at Thisted (107 and 140 km^2 in 2015, 77 and 96 km^2 in 2016 and 63 and 186 km^2 in 2017). Similarly, for home ranges calculated with MCP (228 and 233 km^2 in 2015, 187 km^2 for both in 2016, 106 and 119 km^2 in 2017). Individual home range sizes were highly variable. Home ranges calculated with BBMM (95%) ranged from 5 km^2 (Töreboda, during autumn 2017) to 261 km^2 (Thisted, wintering area during 2016). The core area (50%UD) ranged from 1 to 36 km^2 (for the same locations). For the MCP, the range varied from 4 to 244 km^2 (Örebro in autumn 2015 and Thisted in 2017 respectively). No correlation was found between home range size and number of locations per home range (r_s= 0.16, P=0.153).

Table 2: Median home ranges in km^2 of all three years recorded as calculated by BBMM (Brownian Bridge Movement Models) 50% and 95% UD as well as MCP (Minimum Convex Polygon). Home ranges are shown for every major stopover site: Töreboda (separated in spring and autumn), Åsnes (visited only by the two Norwegian breeding birds during spring) and Örebro during autumn as well as the wintering area in Thisted.

Period	Location	Year	BBMM 95%	range	BBMM 50%	range	MCP	range	n
Spring	Töreboda	2016	11	7 -51	1	1 - 4	11	5 - 100	10
		2017	11	5 – 26	2	1 - 3	11	6 - 59	7
	Åsnes	2016	10	9 – 10	2	2 - 2	5	5 – 6	2
		2017	10	8 -12	2	2 - 2	12	8 – 15	2
Winter	Thisted	2015	97	42 – 209	18	7 - 31	98	21 - 234	10
		2016	77	32 – 261	15	4 - 36	92	25 - 217	9
		2017	75	26 – 186	11	4 - 24	95	29 - 244	8
Autumn	Töreboda	2015	66	44 – 100	9	6 - 22	80	8 - 154	11
		2016	49	11 – 77	7	2 - 11	72	6 – 93	8
		2017	63	30 – 116	9	3 - 12	101	75 - 116	7
	Örebro	2015	10	10 – 54	2	2 - 3	12	4 – 21	3
		2016	25	20 – 27	3	3 - 4	31	20 - 32	3

To give an indication of how similar the home ranges are of geese residing at the same stopover (during the same period) the overlap percentage was also determined in table 3. Overlap ranged from 0% to 95%. For each stopover I also calculated the amount of overlap of each individual goose had when returning in a subsequent year (table 4). Percentage of overlap from all stopovers ranged from 22.8% to 83.7%, meaning that all geese showed at least some degree of similarity between years. Both the Norwegian and northern Sweden breeding birds had used Thisted as their wintering grounds. When comparing the combined home ranges of the northern Sweden breeding birds against the joined home ranges of the two Norwegian birds at Thisted, these two groups had an overlap of 40.9%, 35.3% and 32.3% in the three subsequent years recorded.

Table 3: The median home range overlap index for geese utilising the same stopover during the same period (overlap within season). The stopovers included are: Töreboda (during both spring and autumn), Åsnes (spring), Örebro (autumn) as well as the wintering grounds in Thisted. Overlap index ranges from 0 (no overlap) until 1 (100% overlap).

Period	Location	Year	Median overlap index within season	range	n
Spring	Töreboda	2016	0.36	0 - 0.82	10
		2017	0.42	0.10- 0.80	7
	Åsnes	2016	0.86	-	2
		2017	0.87	-	2
Winter	Thisted	2015	0.06	0 - 0.92	10
		2016	0.07	0 - 0.90	9
		2017	0.05	0 - 0.78	8
Autumn	Töreboda	2015	0.70	0.08 - 0.86	11
		2016	0.62	0 - 0.90	8
		2017	0.75	0.60 - 0.95	7
	Örebro	2015	0.52	0.51 - 0.80	3
		2016	0.72	0.67 - 0.76	3

Table 4: The median overlap index between subsequent years (between years) for Töreboda (during spring and autumn), Åsnes (spring), Örebro (autumn) and the wintering grounds in Thisted. Overlap index ranges from 0 (no overlap) until 1 (100% overlap).

Period	Location	Years	Median overlap index between years	range	n
Spring	Töreboda	2016 - 2017	0.56	0.41 - 0.82	7
	Åsnes	2016 - 2017	0.61	0.60 - 0.61	2
Winter	Thisted	2015 - 2016	0.61	0.29 - 0.82	9
		2016 - 2017	0.57	0.22 - 0.72	8
Autumn	Töreboda	2015 - 2016	0.72	0.25 - 0.84	8
		2016 - 2017	0.76	0.67 - 0.81	6
	Örebro	2015 - 2016	0.45	0.43 - 0.48	2

4 Discussion

Tagged Taiga Bean Goose moulting in Vilhelmina, Sweden were revealed to have two distinct migratory paths. The majority flew to Töreboda to stage during spring before flying to their breeding grounds in Västerbotten County. Two tagged geese migrated along the Swedish-Norwegian border and had separate breeding grounds in Børgefjell national park.

Home ranges calculated by MCP (100%) for wintering Taiga Bean Geese in Slamannan, Scotland were found to be on average 23.5 (±1.0) km^2 (Mitchell et al., 2016). Studies calculating home range sizes (with 100% MCP) for other goose species have cited: sizes ranging from 4.0 to 69.5 km^2 for Barnacle Geese (*Branta leucopsis*) wintering in Scotland (Phillips et al., 2003), and home range sizes varying from 5.8 to 9.2 km^2 for Canada Geese (*Branta canadensis*) tracked with VHF during their winter period in South Carolina (Giles, 2010). In comparison, Taiga Bean Geese in this study were shown to cover a much larger area during winter with sizes ranging from 21 until 244 km^2 (table 2). The larger total areas covered are not the result of exploratory trips made by the geese when observing the location data. In addition, the core areas used by geese, calculated with BBMM (50%), are also seemingly also quite large. Also, all geese had several core areas, indicating they most likely have multiple feeding areas and roosts. Home range sizes are highly flexible and are mostly dependent upon food availability and habitat (Rolando, 2002; Schoener, 1983). In this study, we did not focus on factors such as field use. In the future, it would be interesting to determine whether factors such as this or depletion due to competition or perhaps increased disturbance might have contributed to larger home ranges. Currently Taiga Bean Geese are protected from hunting in Thisted, but other goose species are still hunted upon and subjected to scaring techniques (Marjakangas et al., 2015). Separating the Taiga Bean Goose from similar looking goose species is also notoriously difficult in the field. However, these numbers should be somewhat treated with cation. Individual home ranges are highly variable, and the home ranges in this study are based upon a limited number of geese.

Most tagged geese left their wintering grounds around the beginning of March. Comparing these departure dates to the prevalence of Bean Geese in Denmark (DOFbasen, 2018) show that these are not out of the ordinary. Though arrival dates were a bit more variable, most arrived in December and were comparable to the increase in sightings in Denmark. Töreboda was found to be the main spring staging site used by the birds breeding in southern Västerbotten. Geese adopt a (partial) capital breeding strategy (Clausen et al., 2003; Glahder et al., 2006; Klaassen et al., 2006), i.e. they rely on energetic reserves acquired at stopovers along the way for breeding. Like is the case with our Swedish breeding birds, spring migration is thought to commonly be shorter than autumn migration (Nilsson et al., 2013). The Norwegian breeding birds however consistently defied this rule. Several studies have noted that this rule is not always applicable to larger species, particularly waterfowl (Kölzsch et al., 2016; Schmaljohann, 2018). A key factor in spring migration timing is food availability, and geese are known to stepwise follow the so called 'green wave' of spring growth (van der Graaf S.A.J. et al., 2006; van Wijk et al., 2012). Unfavourable conditions at their breeding grounds such as ice cover also potentially delays the duration of migration during spring (Nuijten et al., 2014). A number of geese did indeed make early exploratory movements later in the season to their breeding before returning to stopovers close by. Why the two individuals breeding in Norway seemingly adopt a different strategy compared to the Swedish breeding birds is not entirely clear. Birds are known to bypass stopovers during the return trip which have been used on their way to their breeding grounds due to differing food qualities later on in the season (Beekman et al., 2002). While the Swedish breeding birds made at least one long term stopover at Töreboda, the two tagged geese from Norway flew straight to their wintering grounds during early September. Tagged goose with id "svan05" departed approximately a month later (27th of September) in 2017 from Børgefjell, also making several short-term stopovers along the way. Rather than refuelling, these short stopovers were most likely made for drinking or resting. This particular female was accompanied by juveniles during that year (appendix I). Typically, non-breeders arrive earlier during the season compared to family groups (Gundersen et al., 2017; Reed et al., 2003). But little is yet known how individual migratory behaviour is affected by being accompanied by juveniles (if at all), and whether this might have contributed to the slightly longer (5 days) and delayed autumn migration, and use of several short-term stopovers. Unfavourable wind conditions could also have been a contributing factor (Beekman et al., 2002; Shamoun-Baranes et al., 2003). Nonetheless, autumn migration for svan05 during 2017 was still considerably shorter compared to the Swedish breeding birds.

Only two individuals opted for wintering in southern Sweden and Zealand in Denmark. Although the exact proportion of birds breeding in Västerbotten which winter in southern Sweden is not entirely clear, the majority of the population wintering in these areas are thought to consist of birds breeding in northern Fennoscandia (Marjakangas et al., 2015; Nilsson, 2011).

All birds wintering in Thisted returned in the following years. Returning to the same site, the Taiga Bean Geese also displayed a high degree of similarity in space use compared to previous years. This tendency for high site fidelity, i.e. philopatry, is well documented in goose species (Kruckenberg and Borbach-Jaene, 2004; Robertson and Cooke, 1999; Wilson et al., 1991). Strong persistence to a site can leave a population vulnerable, especially when a certain site harbours a majority of that population. The two Norwegian breeding birds were also remarkably consistent in their fidelity to their wintering and stopover sites. Previously tagged Taiga Bean Geese breeding in the Børgefjell area were similarly found to winter in the same area in Thisted (Kroglund and Østnes, 2016).

Previous telemetry data indicates similar use of stopover sites with the Taiga Bean Geese wintering in central Scotland (Mitchell et al., 2016) at Thisted and partially in Norway (Åsnes). Taiga Bean Geese which either cross or fly closely along the Gulf of Bothnia to breed in the very northernmost of Fennoscandia also commonly reside at the Töreboda stopover (Ole Roland Therkildsen, pers. com., see also Paasivaara, 2012). Despite the connectivity during certain parts of the migratory cycle, these flyways are seemingly separate with distinctive breeding areas. So just how separate are these flyways? Geese pass on migration strategies amongst themselves socially (Harrison et al., 2010; Sutherland, 1998). This cultural transmission from parent to offspring can have consequences for genetic structures within a population. Strong traditions can limit gene flow between populations and thereby enhance divergence, even when no physical barriers are present. Genetic samples taken from birds at Røyrvik municipality (Børgefjell) in Norway as well as Nästansjö and Stalon in Sweden have revealed the occurrence of at least two subpopulations, each genetically distinct (De Jong et al., 2018). This study did find that birds originating from the Børgefjell area were more genetically distant from those from the Nästansjö than the Stalon area, but location alone could not entirely account for the genetic variation. Instead, the study attributes this to Taiga Bean Geese of different subpopulations utilising the same site during the moulting period. Indeed, the telemetry data confirms that both birds breeding in the Børgefjell area and in northern Sweden utilise Stalon as a moulting site, but the two birds from Børgefjell did not visit Nästansjö. The Norwegian breeding population from which the two Norwegian breeding tagged geese originate is thought to currently consist of only 30 to 60 pairs of Taiga Bean Geese, most of which reside in Finmark (Kroglund and Østnes, 2016). Our data confirms that during winter, the Swedish and the Norwegian breeding birds have overlapping utilization distributions at their wintering grounds in Thisted. Little is yet known about timing of pair formation in geese, but it is to also occur during winter (Owen et al., 1988). Geese social structures are complex, and despite the overlap (also during the apparent pair formation period) Taiga Bean Geese wintering at Thisted show at least two separate sub-populations.

Although the sample size for the Norwegian birds only consisted of two individuals, the consistent discrepancy in migratory behaviour during three years combined with recent genetic evidence indicates that these birds can be considered largely distinct from the Swedish breeding birds. This highlights the importance of not only identifying key stopover sites, but also the connectivity of these areas between winter and breeding grounds. Uncovering discrete migratory routes is thus crucial for implementing more targeted conservation efforts towards more vulnerable subpopulations. Field surveys targeting the key stopover sites should contribute further to knowledge regarding the amount of geese utilising a particular route. It is also worth noting that despite high philopatry, migratory behaviour is complex and not always entirely static. Cultural transmission of migration can potentially adjust rapidly according to changing environments (Clausen et al., 2018; Jonker et al., 2013). It is therefore vital to continue to monitor migratory behaviour to identify any possible changes that occur. Especially in light of recent global warming events, Taiga Bean Geese from the CFU for instance have increasingly opted for wintering in more northern areas (Sweden and Denmark), as opposed to Germany and the Netherlands. This shift is also related to the changing land use in Denmark, which has increased its cultivation of winter cereals (Fox et al., 2005). Encompassing 3 years of telemetry data, this study contributes towards a first step in better understanding the delineation and connectivity of flyways of Taiga Bean Geese breeding in Scandinavia.

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Appendix I

Summary of GPS-collars. "Last download" indicates the last date at which a goose was alive or transmission was received. Years in which an individual goose was confirmed to have juveniles by sightings are shown in bold.

GPS collar code	Neck band	Deployment	Last download	Sex	Age	Number of days recorded	Number of GPS data points	Tracks[a]	Ringing location[b]	Nesting attempt?
SLU02	s2	17-Jul-14	12-Jun-16	?	2CY	548	3899	s,a	A	2016
SLU06	s6	18-Jul-15	4-May-17	M	A	653	5439	s,s,a,a	H	
SLU08	s8	18-Jul-15	30-Apr-18	F	A	1013	7585	s,s,a,a,a	H	
SLU09	s9	18-Jul-15	30-Apr-18	M	A	985	9617	s,s,a,a,a	H	2016
SLU11	s11	18-Jul-15	30-Apr-18	F	2CY	964	8001	s,s,a,a,a	H	2017
SLU12	s12	18-Jul-15	30-Apr-18	F	2CY	972	10482	s,s,a,a,a	H	
SLU13[c]	s13	18-Jul-15	30-Apr-18	F	2CY	674	3540	s,s,a,a	H	
SVAN01	s14	18-Jul-15	30-Apr-18	F	2CY	990	6526	s,s,a,a,a	H	
SVAN03	s16	18-Jul-15	5-Jun-16	F	A	313	1776	s,a	H	
SVAN04	s17	18-Jul-15	30-Apr-18	F	A	1017	7027	s,s,a,a,a	H	2016,2017
SVAN05	s18	19-Jul-15	30-Apr-18	F	A	991	6287	s,s,a,a,a	E	**2017**[d]
SVAN06	s19	19-Jul-15	30-Aug-17	F	2CY	766	4774	s,s,a,a	E	**2016**[e], 2017
SVAN07	s21	19-Jul-15	30-Apr-18	F	2CY	899	4982	s,s,a,a,a	E	

[a] s = spring, a = autumn

[b] A = Arasjön, H = Heligfjäll and E = Eriksberg all in Vilhelmina, Sweden

[c] Autumn migration 2016 is excluded due to missing GPS records.

[d] Had offspring in 2017 (Jan Eivind Østnes, pers. com.)

[e] Sighting confirmed by geese.org

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