Moult migration of Northwest Mainland European Whooper Swans *Cygnus cygnus*

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Abstract

Moult migration routes taken by non-breeding individuals from the Fennoscandian subpopulation of the Northwest Mainland European Whooper Swan *Cygnus cygnus* population were determined by tracking swans fitted with data loggers in Lower Saxony, Germany, during 2014. Depending on their origin, the swans flew between a few hundred and many thousands of kilometres (maximum distance: 2,323 km), to reach moulting sites in the Russian Arctic (at latitudes above 66.57°N) within the Nenets Autonomous Okrug and the Yamalo-Nenets Autonomous Okrug. The stages (distance travelled without stopping) of the moult migration were typically far shorter (mean ± s.d. = 34.9 ± 39.6 km) than those flown during spring migration (114.1 ± 133.4 km) or on autumn migration (204.6 ± 248 km). The mean flying height during moult migration (52.1 ± 47.6 m) also differed from that recorded in spring (146.8 ± 136.9 m) and autumn migrations (280.1 ± 350.5 m).

Key words: data logger, flight altitude, long-distance migration, moulting, Whooper Swan.

Since the mid-20th century, the Northwest Mainland European population of Whoopers Swans *Cygnus cygnus* has increased markedly, both in terms of the numbers of individuals and in their geographic range (Brazil 2003; Laubek *et al.* 2019). Whilst the wintering and breeding movements and distributions have received considerable attention from researchers (*e.g.* Mathiasson 1991; Luigujõe *et al.* 2002; Nilsson 2002), moulting sites have been less well studied (but see Boiko & Kampe-Persson *et al.* 2012; Boiko & Wikelski 2019). Breeding birds that hatch a brood successfully generally stay in their breeding area for the whole summer to raise their offspring, with moulting typically occurring in the vicinity of the breeding site (Einarsson 1996; D. Boiko, pers. comm.; N. Stenschke, pers. obs.). Yet within Whooper Swan populations non-breeding birds, whose moulting sites are largely unknown for much of Eurasia, can account regionally and annually for 35–80% of the total population (Haapanen *et al.* 1973; Haapanen

1991; Matthiasson 1991; Shchadilov *et al.* 2002).

Among the non-breeding swans, different moulting strategies can be observed, depending on the population and breeding location. Non-breeding swans in the Icelandic Whooper Swan population may moult in relatively small numbers on lakes occupied by breeding pairs, but they also congregate in large groups of several hundred or even over 1,000 individuals (Einarsson 2002), possibly due to the geography of Iceland (since the island offers limited possibilities for more extensive migration; Brazil 1981), although the location and abundance of food resources will also influence the size and distribution of the moulting flocks. In contrast, within Finland in large parts of the breeding habitat only small groups of non-breeders (≤ 10 individuals) can be found (Haapanen 1991). The lack of important moulting grounds found within Fennoscandinavia suggests that the non-breeding birds stay for only a few weeks at sites used in early summer before moving to an as yet unknown moulting area (Boiko & Kampe-Persson 2012). Moulting flocks of Whooper Swans have been observed further east in the Russian Arctic, such as on the delta of the Pechora River and Korovinskaiya Bay of the Nenetskiy National Okrug (Shchadilov *et al.* 2002) but the migration routes taken by most of these birds are unclear. The aim of this study, therefore, is to improve our understanding of the movements and sites used by the Northwest Mainland European Whooper Swan population, and particularly to describe their migration to the moulting grounds.

Material and methods

In order to provide the location data needed to describe the migration routes followed by Whooper Swans wintering in northwest Europe, 12 collar-integrated data loggers were developed by Theo Gerrits (www.madebytheo.nl) for tracking individual birds. The housing used to hold the loggers (70 mm in length, 40 mm in width and 11 mm in height) was produced by means of 3D printing and was attached (glued) to a standard neck-collar (57 mm diameter, 80 mm in height). Six solar cells, located on the outside of the housing, supplied electricity to an internal battery which powered the loggers. The yellow neck-collars were each inscribed with an alphanumeric code (characters 30 mm high), with number-letter-number-number combinations, which could be read at distances of up to 1,000 m with a telescope (based on our own trials). The total weight of the logger and collar was *c.* 45 g.

Provided there was sufficient energy in the battery, the data loggers recorded and saved two coordinate sets (*i.e.* a pair of coordinate sets) every 15 min via GPS. The two coordinate sets were recorded at 10 s intervals. Data recorded were: current date (in year-month-day format; DATE), current time (in hours:minutes:seconds format; TIME), position longitude (in whole degrees, default World Geodetic System 1984 (WGS84); LONDEG), position latitude (in whole degrees, default WGS84; LATDEG), altitude above mean sea level (in metres; ALTMSL), ground speed (in m/s; SOG), course in degrees 0.359° (COG), position accuracy (HDOP), number of satellites used to determine position (SV), time to fix position (in secs; TTF), battery voltage (in volts; VBAT) and core temperature (in °C).

All coordinate sets from a data logger were treated as the dataset for that individual bird. During sufficient energy supply (*i.e.* a fully charged battery) 192 coordinate sets (*i.e.* 96 pairs of coordinate sets) could be stored per day. Battery power depended on ambient temperature, cloud coverage, and the orientation of the solar cells. To download the data, every swan with a logger had to be found and approached to within at least 600 m. The logger could then be contacted and the data downloaded to computer (using PuTTY software) via an antenna and Bluetooth.

Catching and selection of swans for tagging

Whooper Swans wintering near Vörden, Lower Saxony, Germany (52.47°N, 8.12°E) were caught by cannon-net on 26 January 2014 and 4 February 2014. The birds were all measured (head length, wing length), weighed and fitted with a metal leg-ring from the Helgoland bird ringing station and with a neck-collar. Some of the collars also had the collar-mounted GPS logger. Age and sex were determined from plumage characteristics (age) and cloacal examination (sex), respectively. Selection of the birds to be fitted with loggers followed pre-defined criteria. At least half of them had to be young animals (*i.e.* in their first winter) in order to determine the movements of sub-adults and to identify moulting grounds not on breeding territories, as Whooper Swans rarely breed before at least 2 years of age (Einarsson 1996). Adult females of unknown precise age (*i.e.* with all-white adult plumage) were also equipped with a logger to determine possible nesting sites. Most adult males were fitted only with a metal leg-ring and a collar without a logger, to avoid duplicate migration tracking of paired birds (*e.g.* the paired birds 6R53 and 9R03, see below); however, one adult male was equipped with a logger. Overall, nine Whooper Swans were caught, of which six were fitted with a data logger on 26 January 2014, whilst on 4 February 2014 another 13 Whooper Swans were caught and six were allocated loggers (Table 1); hereinafter referred to as logger-equipped birds. The loggers' coordinate sets were supplemented by various parameters from the www.movebank.org website, where parameters such as weather or geographical data could be added automatically to the coordinates data. In particular, the Whooper Swan tracking data were supplemented with two parameters using the "EnV-DATA" annotation service (Dodge *et al.* 2013): 1) the land or ocean floor elevation (*i.e.* ETOPO1 Elevation), which gives the elevation (in metres a.s.l.) of the land surface above sea level and the ocean floor below sea level, and 2) the elevation over ice (*i.e.* ETOPO1 Ice Surface Global Relief Model), both accessed via the NOAA National Geophysical Data Center (http://www.ngdc.noaa.gov/mgg/global/; Amante & Eakins 2009). Subtraction of the altitude data recorded by the loggers (above mean sea level) from the land elevation data, thus gave the birds' actual (above ground) flight height over terrestrial terrain. For the current study this calculation was

Table 1. Data associated with all Whooper Swans equipped with a logger. 6R53 and 9R03 are mates and the parents of 9R04, 9R05 and 6R83 (6R83 without logger). K2 = second calendar year; K3 = third calendar year; immat. = immature bird (at the time of ringing in third calendar year).

Logger code	Banding date	Sex	Age	Parents	Siblings	Wing length (mm)	Weight (g)
9R00	26 Jan. 2014	Male	Juvenile (K2)			582	9,600
9R01	26 Jan. 2014	Female	Adult			590	8,710
9R02	26 Jan. 2014	Unknown	Immat. (K3)			599	9,300
9R03	26 Jan. 2014	Female	Adult			580	10,280
9R04	26 Jan. 2014	Male	Juvenile (K2)	6R53, 9R03	9R05, 6R83	583	10,650
9R05	26 Jan. 2014	Male	Juvenile (K2)	6R53, 9R03	9R04, 6R83	592	10,260
9R06	4 Feb. 2014	Male	Immat. (K3)			607	9,790
9R07	4 Feb. 2014	Male	Adult			615	9,760
9R08	4 Feb. 2014	Female	Adult			570	8,160
9R09	4 Feb. 2014	Female	Adult			588	7,780
9R10	4 Feb. 2014	Female	Adult			588	8,320
9R11	4 Feb. 2014	Female	Adult			598	8,130

made exclusively for migration events during spring, moult and autumn migration; altitude of flights recorded when the swans remained at one place for several days (*e.g.* at wintering sites, main staging sites or on the breeding grounds) were omitted from the flight height analyses.

Each coordinate set was assigned to a migration state category. As no algorithms on the particular categories exist, the specifications were added manually to every 133,000 coordinate sets. Therefore every coordinate set received one of the eight following additional specifications relating to the position or current behaviour of the bird. The Whooper Swans' annual cycle can be grouped into eight main phases, according to the stage of migration, as follows:

I. Wintering (= *at wintering site*)
II. Spring migration (including at staging sites)
III. Summer (breeders = *on breeding grounds territories*; non-breeders = *at summer non-breeding sites, which may be adjacent to breeding territories*)
IV. Moult migration (does not apply to breeding birds, because they moult on their breeding territories)
V. On arrival at the moulting site (= *pre-moult phase*)
VI. Moult
VII. Time between the end of moult and onset of autumn migration, in the vicinity of the moulting site (= *post-moult phase*)
VIII. Autumn migration (including at staging sites).

Phases II, IV and VIII can be interrupted by several short or long stopover periods, with the birds spending several days or weeks at a site to rest and regain energy reserves needed for onward migration (*e.g.* Nolet & Drent 1998). A distinction is made between short flight stops with a duration of < 24 h and stopovers of > 24 h. Migration stages can be flown over just a few days or even a few hours. Phase IV is omitted for breeding birds, because the birds moult on their breeding territories (Scott *et al.* 1953; Einarsson 1996) and are generally thought to start their autumn migration from near there. Among the logger birds, this affected only swan 9R03.

Having determined all flight events, the minimum and maximum duration of migratory flight (excluding time spent replenishing energy reserves at staging sites) could be calculated for individual swans. The minimum flight duration of a migration event (*i.e.* the spring, moult or autumn migration) was determined by summing the duration of all flight stages for each migration and adding a factor to allow for the time (not recorded by a logger) between departure and the first coordinate recorded during the flight, and between the last coordinate in flight and landing. Since there are a maximum of 15 min between each pair of coordinate sets, 15 min was added to each stage (7.5 min each for departure and landing). The maximum duration of flights resulted from the sum of all durations between first and last coordinates of a flight. Every stage of a flight (including those without coordinates recorded in flight) was identified and each swan's distance travelled was ascertained (by use of distance calculation between two coordinates in Microsoft Excel 2007).

To classify the moult phase, the logged data suggests that all four swans covered only very short distances (< 150 m between each coordinate), and this was used to classify the start of the actual moulting phase. Following this phase, it was possible to document how the swans covered ever increasing distances and engaged in a few short flights. A distance of more than 1,000 m between two sets of coordinates marked the beginning of the post-moult phase, since the bird had probably regained its flying abilities and consequently the wing moult was completed; this was documented for each of the logger-equipped birds.

Results

During the winter of 2014/2015, five birds fitted with data loggers were sighted and their data downloaded, which were taken as a basis for the current study (Fig. 1, Table 2). Four of the five tracked swans undertook a moult migration, as defined by Salomonsen (1968), with the birds occasionally covering large distances during their migratory flights (Fig. 2). The moult migrations recorded for each individual are described in further detail below.

Whooper Swan 9R02 (immature; sex not known). On 19 May, 9R02 left its summer

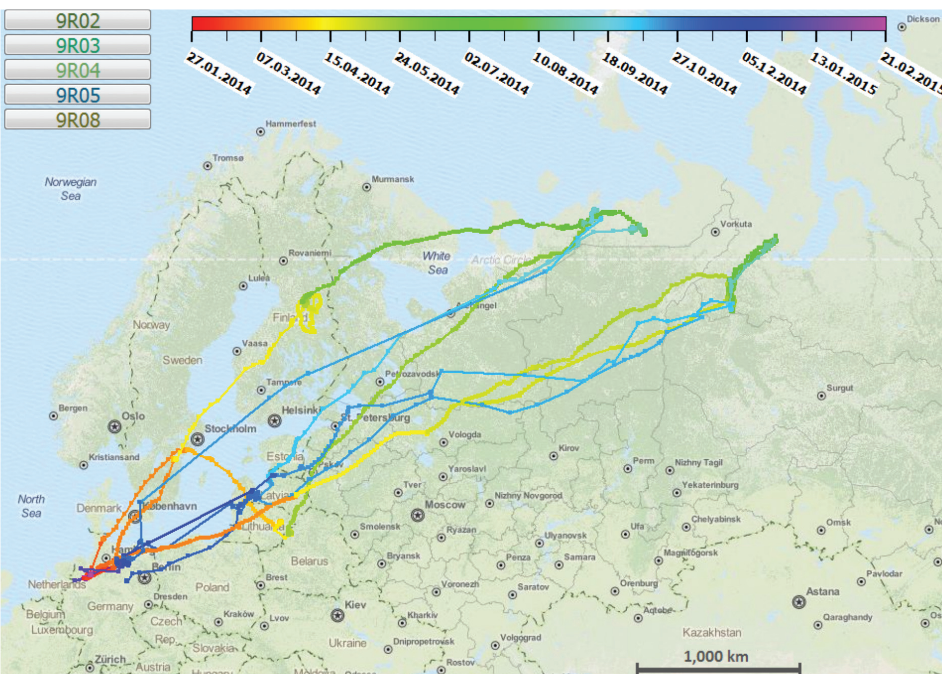

Figure 1. Overview of the study area and the return (spring and autumn) migration routes taken by all five Whooper Swans fitted with GPS loggers. Changes in colour on the swans' tracks illustrate changes in date. Source: OpenStreetMap licence CC BY-SA (https://www.openstreetmap.org/copyright).

Table 2: Quality and quantity of data retrieved from the loggers between 27 January 2014 and 21 February 2015. The mean number of coordinates recorded per day was calculated by dividing the total number of coordinates by the number of days with data for each logger. * = downloads ceased because of extremely low battery power, so data were available only until 2 August 2014.

Logger code	Start of recording	Last download	No. of days	No. coordinates	Mean no. coordinates per day
9R02	29 Jan. 2014	29 Dec. 2014	335	24,514	73.2
9R03	27 Jan. 2014	1 Dec. 2014*	188	27,427	145.9
9R04	27 Jan. 2014	13 Nov. 2014	291	27,420	94.2
9R05	28 Jan. 2014	21 Feb. 2015	390	29,229	74.9
9R08	4 Feb. 2014	21 Feb. 2015	383	24,141	63.0
Total			1,587	132,731	83.6

habitat in Belarus and flew in a northeast direction, covering (with a few exceptions) short distances (8–50 km) during the night and resting during the day until 24 May (Fig. 2). Four non-stop flights were of > 100 km each, but never exceeded 190 km. From 24 May onwards, it also flew during the day. One stage amounted to 124 km; the remaining flights were of < 50 km. Prior to 1 June, 9R02 rested for > 24 h on two occasions (for 30.5 h and for 49.5 h) and often alternated short flights with short resting periods. From 1–19 June it rested in the Pechora Delta, 20 km northwest of the city of Naryan-Mar in the Nenets Autonomous Okrug region of Russia. After 19 days, it flew 70 km in a north easterly direction to the mouth of the Pechora River and continued heading east. After another 60 km, it changed course again and flew 120 km to the southeast. On 21 June it reached the moulting site (at 67.474°N, 57.691°E), located in the Nenets Autonomous Okrug region, *c.* 120 km south of the Pechora Sea and 250 km northwest of the Ural Mountains in Northern Siberia. Hence, 9R02 flew 2,323 km (linear distance: 2,158 km) to its moulting grounds (Appendix 1). On 16 September 9R02 headed 45 km northwest from its moulting site to start migration to the wintering grounds, reaching Germany at the beginning of November.

9R03 (breeding adult female). Individual 9R03 was one of the five logger-equipped swans for which a breeding site could be determined. 9R03 (the parent of 9R04, 9R05 and 6R83) returned to her breeding site in spring 2014, which was located in the same area as the summer habitat of 9R04

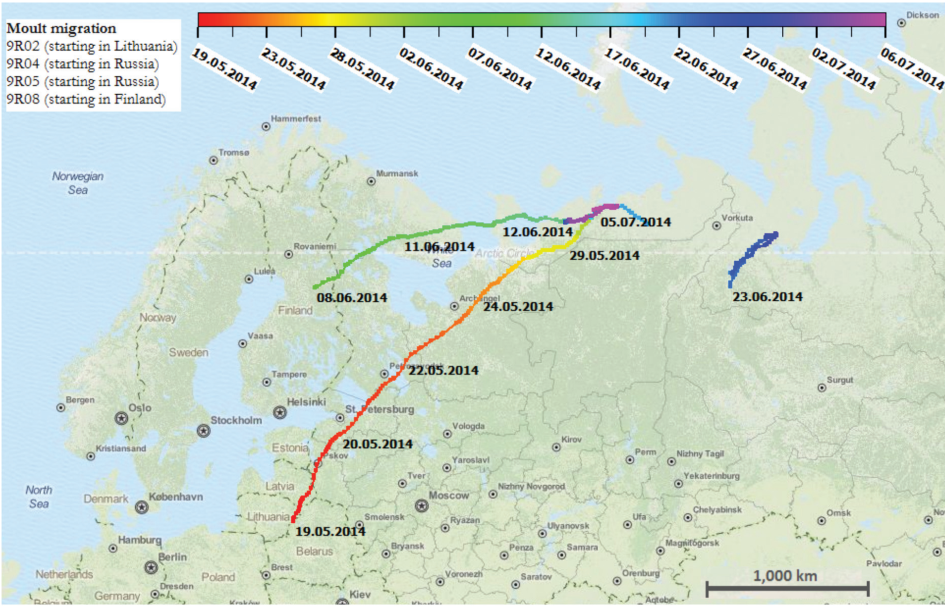

Figure 2. Moult migration routes of 9R02 (starting in Belarus), 9R04 and 9R05 (east of the Urals) and 9R08 (starting in Finland). Change in colour on the tracks illustrates the change in timing. Source: OpenStreetMap licence CC BY-SA (https://www.openstreetmap.org/copyright).

and 9R05, *c.* 130 km east of the Urals on the West Siberian Plain in Yamal-Nenets Autonomous District, 25 km east of the village Muzhi (65.385°N, 65.251°E). The river system of the Lower Ob is nearly 43 km wide and about 400 km long before it enters the Kara Sea (part of the Arctic Ocean). The breeding habitat had few open water areas and was otherwise covered by vegetation, which was ideal for breeding Whooper Swans (Johansen 1959). 9R03 stayed exclusively in that habitat from 1 May to 2 August 2014. There were no further data recorded after 2 August 2014, as the connection to the logger was disrupted during download and could not be restored later. Since Whooper Swans nesting in Iceland, the Baltic Countries, and Germany are all very faithful to their breeding sites (Einarsson 2002; D. Boiko pers. comm.; N. Stenschke, unpubl. datas), these areas were very likely the natal site of 9R04, 9R05 and 6R83 in 2013. Another indication was that 9R04 and 9R05 briefly visited this area ten days after their parents, even though they both used different routes during spring migration. This was an enormous orientation achievement by these birds, given the vastness of the Lower Ob region.

9R04 and 9R05 (juvenile males). Both 9R04 and his sibling 9R05 migrated to east of the Ural Mountains and moulted *c.* 300 km (linear distance) north of their summer habitat (Fig. 2). Their main summer site was within the catchment of the Rivers

Schuchya and Khadytayakha, at the southwest border of the Yamal Peninsula, *c*. 40 km from the most northern section of the delta of the River Ob. As for 9R02, the individual flight stages during moult migration of both birds were short. 9R04 left its summer habitat on 22 June and covered two slightly longer stages of 72 km and 77 km on flying the 330 km to its moulting grounds during 23, 24 and 28 June. From 25–27 June it rested 25 km east of its destination, which it reached on 28 June (67.228°N, 65.298°E). Between each flight it rested for several hours. Subsequently, the swan left its summer habitat on 7 October, which he had returned to after moulting. 9R05 left the same summer habitat on 21 June, a day before 9R04, and flew in a northerly direction. Its migration route of 401 km was also interrupted by short roosting phases and on several days (21, 24 and 28 June) it covered only short distances (≤ 62 km), before arriving at its moulting site (67.229°N, 69.254°E). After moulting he left this area at the end of August. The distance between the moulting site of 9R04 and 9R05 was only 8 km. After moulting both swans used the same habitat, though not always at exactly the same time.

9R08 (Adult female). 9R08 left its summer habitat in Finland on 8 June and flew in a northeast direction to Lake Pyaozero, within the Republic of Karelia in northwest Russia. It rested for 50 h and covered 900 km between 11–13 June. As with other unpaired swans (seen without a mate in winters 2013/14 and 2014/15) that were tracked during this study, it progressed in short stages and with multiple stops, until it reached Lake Tayvo-To in the Nenets Autonomous Okrug region, 110 km east of Naryan-Mar. On the way, it crossed the Kola Peninsula and proceeded across the Barents Sea to the Kanin Peninsula. Travelling through the centre of the peninsula towards its eastern tip, it then crossed the mouth of Tschoscha Bay thus using the narrowest space between the peninsula and the mainland. Having reached the coast, it turned north east, flew at a distance of 9 km from the shore into the Indiga Bay and reached the mainland 17 km northwest of Indiga. After flying another 70 km in a southeast direction it reached Lake Tayvo-To, whereupon it rested at the lake for three weeks, before arriving on the moulting grounds in Golodnaya Bay on 4 July. During the next few days it left the moulting grounds temporarily, crossing the Pechora River delta and continuing to Bolvanskaya Bay, before turning around 127 km northeast of its moulting site and returning to Golodnaya Bay. Having arrived back at Golodnaya Bay on 7 July it did not leave again until 30 August. Overall, 9R08 flew a total distance of 1,449 km (linear distance: 1,108 km) to its moulting grounds. The particular moulting site was located at the south-west tip of Golodnaya Bay (67.783°N, 52.266°E), directly bordering the Pechora Delta and 37 km west of Naryan-Mar in the Nenets Autonomous Okrug.

All four moulting sites were located north of the Arctic Circle (north of 66.57°). The most northerly of the moulting sites was that of 9R08, which was 135 km inside the Arctic Circle, followed by 9R02 (103 km), 9R05 (76 km), and finally 9R04 which moulted 71 km inside the Arctic Circle. In line with the larger distance between the swans' summer habitat and their moulting grounds, 9R02 and 9R08 began their moult migration earlier (19 May and 8 June 2014, respectively) than 9R04 and 9R05 (23 June and 22 June 2014, respectively).

Pre-moult, moult and post-moult periods

All four swans (9R02, 9R04, 9R05 and 9R08) stayed in close proximity to their moulting grounds for several days during the pre-moult period, ranging widely across the surrounding waters, probably mostly swimming rather than flying. For swan 9R02, short flight movements (altitude data) were logged immediately prior to moulting. This period could be clearly identified in the data of 9R02 and 9R04; for 9R05 and 9R08 the onset of moulting could not be determined precisely, but could be assumed on the basis of the sudden short distances recorded between coordinates. Minimum estimates of the duration of the moulting periods varied between the four birds: 9R02 = 36 days, 9R04 = 35 days, 9R05 = 30 days, 9R08 = 21 days.

Various behaviours could be documented during the post-moult phase. 9R04 and 9R05 flew back to their summer habitat and stayed until the beginning of the autumn migration. 9R02 and 9R08, however, remained within 50 km of their moulting grounds until the autumn migration.

Since movement southbound follows the moulting phase, it is not defined as a post-moult period, but as autumn migration. This differentiation has not been possible up to now, because only the arrival of the first Whooper Swans in the Baltic States after moulting has been evaluated. The migration and staging events which occur during the intervening period have not previously been assessed for the species.

Discussion

Several studies have demonstrated that Whooper Swans perform a moult migration (*e.g.* Kampe-Persson *et al.* 2012; Boiko & Kampe-Persson 2012), and nearly all non-breeding Whooper Swans leave their breeding grounds in Germany, the Baltic States, and Scandinavia during the moulting period (Degen & Heinicke 2007; D. Boiko pers. comm.; N. Stenschke pers. obs.). However, only a small number of swans fitted with neck-collars in Latvia have been identified to date within Russia (Boiko & Kampe-Persson 2012; D. Boiko pers. comm.), and up to now, the origins of the large numbers of moulting birds in various regions of Russia were largely unknown. Our tracking work demonstrated that Whooper Swans tagged in the same area of Lower Saxony migrate to different regions in continental Europe (Finland: 9R08, Baltic States: 9R02) and also to western Siberia (9R04, 9R05) before flying north of the Arctic Circle to Russia to undergo their annual moult. Two birds, 9R04 and 9R05, flew only a few hundred kilometres from their summering area which is protected as an IBA (Important Bird Area) or critical site under the name of "Basins of the Schuchya and Khadytayakha Rivers" (Wings Over Wetlands UNEP-GEF African-Eurasian Flyways Project 2011) to their moulting grounds, which they could not have visited before. The same applies to Baltic Whooper Swans, which fly to the region of Archangelsk (Russia) to moult (Boiko & Kampe-Persson 2012). This suggests that the long distances covered during moult migration by 9R02 (2,323 km) and 9R08 (1,449 km) to reach the moulting site is innate. Swans 9R02 and 9R08 also began their moult migration earlier than 9R04 and 9R05, but whether this was because they were adults and therefore more familiar with the moulting grounds or a reflection of the distribution of suitable sites in each region, remains to be determined.

Natal and breeding site fidelity has been reported for a number of migratory Anseriformes, with female loyalty to the natal breeding area considered a general rule for monogamous long-lived species such as geese and swans (Rees *et al*. 2005), although differential dispersal of the two sexes is considered important to avoid inbreeding (*sensu* Bateson 1983). Ringed juvenile birds from Germany do this (based on our own observations), as well as birds from the Baltic States (D. Boiko, pers. comm.). One bird with a data logger (9R08) stayed within a limited area in Finland, and another (9R02) frequented the border area between Lithuania and Belarus during summer. Both birds may have been close to their natal sites, particularly for 9R08 who visited the area in two consecutive years. After staying in the area for six weeks (9R02) and eight weeks (9R08) they embarked on their moult migration.

Earlier studies report that the first Whooper Swans arrive in the West Siberian Plain during the first half of May (Vartapetov 1998), and these are probably breeding birds and non-breeders arriving in their summer habitat. Whooper Swans in this study did not reach their moulting grounds until mid-June (earliest arrival: 20 June by 9R02), and began to moult at the beginning of July, which corresponds to observations made in Russia with Brazil & Shergalin (2002) describing flocks of up to 200 birds present in mid-June dispersing into smaller groups (< 10 birds) to moult in early July. This observation closely matches the logger data, since 9R04 and 9R05 initially stayed near their natal site, which became their initial summer habitat, but subsequently left that area during the moulting period. It can be assumed that non-breeders merge into groups during summer, as observed in other regions, including Finland (Haapanen 1991) and Iceland (Brazil 1981; Rees *et al.* 1991; Einarsson 1996). The moulting grounds used by 9R04 and 9R05 in the Siberian tundra consisted of a large number of waterbodies. Due to the brief growing season those are very productive and hence well-suited as moulting habitat (Brazil & Shergalin 2002). The same applies to the moulting grounds chosen by 9R02 and 9R08 in the European Arctic.

New insights were also gained about the specifics of moult migration, with the series of short migratory flights ("stepping-stone" migration) raising questions about the reasons for such behaviour. It is possible that the worn plumage is not fit for use on long distance flights. In general, many different intrinsic and environmental influences can be involved in the timing of moulting (McCleery *et al.* 2007; Dawson *et al.* 2009; Howell 2010). The "restless" moult migration, illustrated by numerous short flights (see Appendix 1), could be evidence that the birds intended to reach their moulting ground rapidly, perhaps in order to guard against the loss of wing feathers and to reach the suitable and safe habitats in time. The largest parts of the routes were covered in only a few days. Stopover periods were only extended north of the Arctic Circle. Such behaviour could be established independently for two birds (which were very likely unrelated), but the sample is quite small, and so further investigations are warranted.

Boiko & Kampe-Persson (2012) defined the moulting phase as follows: pre-moult: 1 May–28 June, moult: 29 June–14 September, and post-moult: 15 September–31 October. Following this definition, the moulting period lasts from 1 May to 31 October, during which time the birds will be unable to fly due to simultaneous moult of primary and secondary feathers (Bauer & Glutz von Blotzheim 1990). On the basis of logger data, it is possible to understand the particular phases of a Whooper Swan's life in detail. The moult migration, the arrival at moulting grounds, the moult itself, and the time after moult can be identified precisely, and thus their onset and duration can be analysed (Appendix 2). Our focal Whooper Swans originated from different geographical regions, which were unknown at the point of capture at the wintering site in Germany. Presumable 9R08 originated from Finland, 9R02 from the border region of Latvia and Belarus, and 9R04/9R05 from the Yamal-Nenets Autonomous District in Russia. As such, no general timescales for each moulting period can be established, and so additional research with an increased sample size is required.

All moulting sites were located in the water-rich Russian tundra. Due to the high disturbance sensitivity of swans during the moulting phase it must be assumed in these areas that minimal anthropogenic disruption occurs. In addition, nutrient-rich waters that provide adequate food resources are a prerequisite for a successful moult (Salomonsen 1968), since the birds are unable to fly and cannot change the site. The birds generally are flightless for 5–6 weeks (Dement'ev 1935). Therefore, 9R05 and 9R08 seem to have a fairly short moulting period. Possibly both birds started to moult and shed their primaries earlier; however, this could not be determined more precisely from our data.

The breeding site for swan 9R03 was located in an important breeding and stopover site for the species (Dvuob'ye), which is protected as an Important Bird Area (IBA). The Whooper Swans in that area are regarded as part of the Black Sea/ East Mediterranean population (Wings Over Wetlands UNEP-GEF African-Eurasian Flyways Project 2011). In 2001, approximately 800 to 2,000 individuals were counted during migration (corresponding to 8% of the flyway population), whilst during the breeding season between 100 and 150 breeding pairs were noted (comprising 2% of the flyway population). The breeding site is located in the middle of a section of the Kunovatsky Nature Reserve, within the Lower Dvuobje Ramsar Site (site number 677; Ramsar Sites Information Service 2015a), which is one of the most important breeding grounds for aquatic birds in the world. During migration periods, up to 500,000 waterbirds roost in this area, which covers 540,000 ha, with ducks and swans at the top of the list of species for which the site has been designated (Ramsar Sites Information Service 2015b).

Between 1989 and 2005, counts of Whooper Swans at the moulting grounds of 9R04 and 9R05 (in the Schuchya and Khadytayakha River Basins) during the breeding season recorded between 150–600 birds (Wings Over Wetlands UNEP-GEF African-Eurasian Flyways Project 2011). Moreover, counts of non-breeders from 1996 to 1998 observed between 900–1,500 individuals (Wings Over Wetlands UNEP-GEF African- Eurasian Flyways Project 2011). This area is also assigned to the Black Sea/ East Mediterranean population, and these numbers represent *c.* 2% of that population. The difficulty in matching particular regions to a flyway population therefore is becoming increasingly apparent, and especially in this part of the Russian tundra it is not yet possible to allocate Whooper Swans to a particular flyway. The logger-equipped birds were first tagged on the wintering areas used primarily by the Northeast Mainland European population, so our findings indicate that two or more flyway populations overlap with each other in this area. It is not certain whether the birds use the same flyway for the whole of their lives. It is possible that some swans may occasionally switch to join other flyway populations and hence change their migration routes. One potential event leading to such behaviour may be the pairing of two individuals from different flyway populations, but this assumption requires further investigation.

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References

Amante, C. & Eakins, B.W. 2009. *ETOPO1 1 Arc–Minute Global Relief Model: Procedures, Data Sources and Analysis*. NOAA Technical Memorandum NESDIS NGDC–24. National Geophysical Data Center, National and Oceanic Atmospheric Administration (NOAA), Boulder, Colorado, USA. Doi: 10.7289/V5C8276M (31.07.2015).

Bauer, K.M. & Glutz von Blotzheim, U.N. 1990. *Handbuch der Vögel Mitteleuropas. Volume 2.* AULA-Verlag, Wiesbaden, Germany. [In German.]

Bateson, P. 1983. Optimal outbreeding. *In* P. Bateson (ed.), *Mate Choice*, pp. 257–277.

Cambridge University Press, Cambridge, UK.

Boiko, D. & Kampe-Persson, H. 2012. Moult migration of Latvian Whooper Swans *Cygnus cygnus, Ornis Fennica* 89: 273–280.

Boiko, D. & Wikelski, M. 2019. Moulting sites of Latvian Whooper Swan *Cygnus cygnus* cygnets fitted with GPS-GSM transmitters. *Wildfowl* (Special Issue No. 5): 228–239.

Brazil, M. 1981. The behavioural ecology of the Whooper Swan (*Cygnus cygnus cygnus).* Ph.D. thesis, Stirling University, UK.

Brazil, M. 2003. *The Whooper Swan*. T. & A.D. Poyser, London, UK.

Brazil, M. & Shergalin, J. 2002. The status and Distribution of the Whooper Swan *Cygnus cygnus* in Russia I: western Russia and western Siberia. *Journal of the Yamashina Institute for Ornithology* 34: 162–199.

Dawson, A., Perrins, C.M., Sharp, P.J., Wheeler, D. & Groves, S. 2009. The involvement of prolactin in avian molt: the effects of gender and breeding success on the timing of molt in Mute swans (*Cygnus olor*). *General and Comparative Endocrinology* 161: 267–270.

Degen, A. & Heinicke, T. 2007. Singschwan *Cygnus cygnus*. *In* T. Heinicke & U. Köppen (eds.), *Vogelzug in Ostdeutschland I – Wasservögel, Teil 1*, pp. 44–56. Ber. Vogelwarte Hiddensee Publication No. 18. Vogelwarte Hiddensee, Schleswig-Holstein, Germany. [In German.]

Dement'ev, G.P. 1935. Birds in Kanin Peninsula. *Collection of Works of the Zoological Museum* 2: 23–55. [In Russian.]

Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S.C., Kays, R., Douglas, D., Cruz, S., Han, J., Brandes D. & Wikelski, M. 2013. The environmental data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. *Movement Ecology* 1: 3.

Einarsson, O. 1996. Breeding biology of the Whooper Swan and factors affecting its breeding success, with notes on its social dynamics and life cycle in the wintering range. Unpublished Ph.D thesis, University of Bristol, Bristol, UK.

Einarsson, O. 2000. Iceland. *In* M.F. Heath & M. I. Evans (eds.), *Important Bird Areas in Europe: Priority Sites for Conservation*, pp. 341–363. Birdlife International, Cambridge, UK.

Einarsson, O. & Rees, E.C. 2002. Occupancy and turnover of Whooper Swans on territories in northern Iceland: results of a long-term study. *Waterbirds* 25 (Special Publication 1): 202–210.

Haapanen, A. 1991. Whooper Swan *Cygnus cygnus* population dynamics in Finland. *Wildfowl* (Special Issue No. 1): 137–141.

Haapanen, A., Helminen, M. & Suomalainen, H.K. 1973. The spring arrival and breeding phenology of the Whooper Swan *Cygnus cygnus* in Finland. *Finnish Game Research* 33: 39–60.

Howell, N.G. 2010. Molt in North American birds. Houghton Miflin Harcourt, Boston, New York, USA.

Johansen, H. 1959. Die Vogelfauna Westsibiriens, III. Teil. *Journal of Ornithology* 100: 60–61.

Kampe-Persson, H., Boiko, D., Morkunas, J. 2012. Distribution and numbers of moulting non-breeding Whooper Swans *Cygnus cygnus* in the Baltic States and South Sweden. *Ornis Svecica* 22: 127–138.

Laubek, B., Clausen, P., Nilsson, L., Wahl, J., Wieloch, M., Meissner, W., Shimmings, P., Larsen, B-H., Hornman, M., Langendoen, T., Lehikoinen, A., Luigujõe, L., Stīpniece, A., Švažas, S., Sniaukstra, L., Keller, V., Gaudard, C., Devos, K., Musilova, Z., Teufelbauer, N., Rees, E.C. & Fox, A.D. 2019. Whooper Swan *Cygnus cygnus* January population censuses for Northwest Mainland Europe, 1995–2015. *Wildfowl* (Special Issue No. 5): 103–122.

Luigujõe, L., Kuresoo, A. & Leivits, A. 2002. Numbers and distribution of Whooper Swans breeding, wintering and on migration in Estonia, 1990–2000. *Waterbirds* 25 (Special Publication 1): 61–66.

Mathiasson, S. 1991. Eurasian Whooper Swan *Cygnus cygnus* migration, with particular reference to birds wintering in southern Sweden. *Wildfowl* (Special Issue No. 1): 201–208.

McCleery, R.H., Perrins, C.M., Wheeler, D. & Groves, S. 2007. The effect of breeding status on the timing of moult in Mute Swans *Cygnus olor*. *Ibis* 149: 86–90.

Nilsson, L. 2002. Numbers of Mute Swans and Whooper Swans in Sweden, 1967–2000. *Waterbirds* 25 (Special Publication 1): 53–60.

Nolet, B.A. & Drent, R.H. 1998. Bewick's Swans refuelling on pondweed tubers in the Dvina Bay (White Sea) during their spring migration: first come, first served. *Journal of Avian Biology* 29: 574–581.

Ramsar Site Information Service. 2015a. Lower Dvuobje site map. Available at https://rsis.ramsar.org/RISapp/files/263/pictures/RU677map1.pdf (last accessed 20 September 2019).

Ramsar Site Information Service. 2015b. Lower Dvuobje site map. Available at https://rsis.ramsar.org/ris/677 (last accessed 26 November 2015).

Rees, E.C., Matthews, G.V.T., Mitchell, C.R. & Owen, M. 2005. Movements and Migrations. *In* J. Kear (ed.), *Bird Families of the World: Ducks, Geese and Swans*, pp. 112–131. Oxford University Press, Oxford, UK.

Rees, E.C., Black, J.M., Spray, C.J. & Thorisson, S. 1991. Comparative study of the breeding success of Whooper Swans *Cygnus cygnus* nesting in upland and lowland regions of Iceland. *Ibis* 133: 365–373.

Salomonsen, F. 1968. The moult migration. *Wildfowl* 19: 5–24.

Scott, P., Fisher, J., Goumundsson, F. 1953. The Severn Wildfowl Trust expedition to central Iceland, 1951. *Report of the Severn Wildfowl Trust* 5: 78–115.

Shchadilov, Y.M., Rees, E.C., Belousova, A.V. & Bowler, J.M. 2002. Annual variation in the proportion of Whooper Swans and Bewick's Swans breeding in Northern European Russia. *Waterbirds* 25 (Special Publication 1): 86–94.

Vartapetov, L.G. 1998. Ptitsy severnoi taigi Zapadno-Sibirskoi ravniny [Birds of northern taiga of West-Siberian Plain]. Nauka, Novosibirsk.

Wings Over Wetlands UNEP-GEF African-Eurasian Flyways Project. 2011. *The Critical Site Network: Conservation of Internationally Important Sites for Waterbirds in the African Eurasian Waterbird Agreement area*. Wetlands International, Ede, the Netherlands and BirdLife International, Cambridge, UK.

Photograph: Whooper Swans during migration through the Gulf of Finland, by Ben Cherry.

Appendix 1. Data on the spring/moult/autumn migration of all logger-equipped birds (between 27 January 2014 and 21 February 2015). The sum of all flight routes during migration also includes the local movements, *e.g.* at roosting places. The actual route length shows the migration route without counting the local movements. Linear distance describes the distance between start- and endpoint during moult migration. The minimum flight duration equals the sum of all lengths of particular flights plus a factor for the time not recorded by the logger between start and first flight coordinate or last flight coordinate and landing (15 minutes per particular flight). The maximum flight duration equals the sum of all durations between beginning and ending of each flight movement. The average flight duration results from the minimum and maximum flight duration.

Swan	Migration	Total no. flight events	No. flight events with coordinate sets	No. coordinate sets during flight	Sum of all flights during migration (km)	Actual length of migration route (km)	Linear distance of migration route (km)	Mean length of particular flights (km)	Mean flight altitude records (m)	Mean flight duration (range) (h)
9R02	Moult	54	46	222	2,405	2,323	2,158	43	61	66 (39–93)
	Spring	20	16	82	2,078	1,758	1,179	88	87	33 (19–47)
	Autumn	23	14	86	3,688	3,198	2,860	139	112	90 (24–156)
9R03	Moult	–	–	–	–	–	–	–	–	–
	Spring	27	26	386	3,023	3,697	3,428	137	168	57 (51–62)
	Autumn	–	–	–	–	–	–	–	–	–
9R04	Moult	19	10	33	347	330	236	17	20	11 (6–15)
	Spring	28	27	293	3,889	3,730	3,429	133	213	68 (48–88)
	Autumn	12	6	60	3,898	3,685	3,293	307	493	90 (40–139)

Appendix 1 (*continued*).

Swan	Migration	Total no. flight events	No. flight events with coordinate sets	No. coordinate sets during flight	Sum of all flights during migration (km)	Actual length of migration route (km)	Linear distance of migration route (km)	Mean length of particular flights (km)	Mean flight altitude records (m)	Mean flight duration (range) (h)
9R05	Moult	15	14	57	443	401	331	27	24	13 (9–17)
	Spring	28	28	289	3,903	3,730	3,429	133	143	61 (49–73)
	Autumn	18	6	42	4,300	3,898	3,500	217	282	450 (32–868)
9R08	Moult	41	28	160	1,492	1,499	1,108	35	51	50 (23–77)
	Spring	32	30	193	2,497	2,481	1,616	78	69	43 (35–51)
	Autumn	16	1	2	3,659	3,337	2,929	209	117	– (max. 729)
Total	Moult	129	98	472	4,687	4,503	3,860	–	–	–
	Spring	135	127	1,243	16,290	15,396	13,081	–	–	–
	Autumn	69	27	190	15,545	14,118	12,583	–	–	–
Average	Moult	–	–	–	–	–	–	35	51	35 (19–51)
	Spring	–	–	–	–	–	–	114	140	52 (40–64)
	Autumn	–	–	–	–	–	–	205	279	210 (32–473)

Appendix 2: Length of phases for each tracked swan. Numbers within the bars indicate the duration in days. I =winter grounds, II = spring migration, III = summer sites for non-breeders/ breeding grounds for breeders, IV = moult migration, V = pre-moult, VI = moult, VII = post-moult, VIII = autumn migration. Phases II, IV and VIII are interrupted by short flight stops of < 24 h and longer stopovers of > 24h. 9R02, 9R04, 9R05 and 9R08 are non-breeders and performed a moult migration. 9R03 is a breeding bird which moulted at its breeding site.