Moulting sites of Latvian Whooper Swan Cygnus cygnus cygnets fitted with GPS-GSM transmitters

DMITRIJS BOIKO^{1,2,*} & MARTIN WIKELSKI^{3,4,5}

¹Natural History Museum of Latvia, Kr. Barona iela 4, Riga, LV-1050, Latvia.

²Institute of Biology, University of Latvia, Miera str. 3, LV-2169 Salaspils, Latvia.

³Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, Germany.

⁴Centre for the Advanced Study of Collective Behaviour, University of Konstanz,

Konstanz, Germany.

⁵Department of Biology, University of Konstanz, Konstanz, Germany. *Correspondence author. E-mail: dmitrijs.boiko@gmail.com

Abstract

Previous studies on Whooper Swan *Cygnus cygnus* cygnets hatched in Latvia have shown that *a*. 99% leave the country each year to moult elsewhere in their 2nd to 6th calendar years. To reveal the exact moulting sites, in 2016 ten cygnets were fitted with 91g solar-powered neck-collar-mounted GPS-GSM loggers. Moulting sites were recorded for four individuals in their 2nd calendar year, and for two of these birds in their 3rd calendar year; four birds in total. All of these moulted at sites in Russia; one was in the Republic of Karelia and three were in the Arkhangelsk Region. The mean average straight-line distance between the hatching and moulting sites was 1,451 km (range = 1,038–2,524 km). Although the data were less comprehensive, another tracked swan probably moulted in the western part of the White Sea in the Republic of Karelia. The conservation of these moulting sites is essential for the Latvian Whooper Swans to thrive.

Key words: cygnet, distribution, GPS-GSM logger, moulting, neck-collar, non-breeder, Whooper Swan.

From some tens of pairs remaining in northernmost Sweden and Finland in the early 1950s (Lammi 1983; Svensson *et al.* 1999), the Fennoscandian Whooper Swan *Cygnus cygnus* population has undergone a spectacular increase, in both range and numbers. Today the species breeds in all countries around the Baltic Sea, and the breeding population numbers *c.* 10,000 pairs (Boiko & Kampe-Persson 2010). In Latvia, the western part of the country has been recognised as the core breeding area ever since Whooper Swans were first recorded nesting there (Boiko & Kampe-Persson 2010). In spite of the rapid growth in the Baltic States' population of swans and increased knowledge about the breeding distribution, there are still a number of unknowns regarding birds from that area, for example, where the birds moult their wing feathers. All swans, geese and ducks shed their wing feathers after the breeding period and consequently lose the power of flight (Salomonsen 1968). The Whooper Swan moults its wing feathers from late June to the middle of September and is flightless for about 5-6 weeks (Dement'ev 1935; Boiko & Kampe-Persson 2012). Among wildfowl, breeding birds usually moult their wing feathers on their breeding grounds whereas non-breeders moult in summer congregations. The Whooper Swan matures slowly and first breeding is usually at 4-6 years old (Einarsson 1996). A high proportion of the population therefore consists of nonbreeding birds, and about two-thirds of the population do not attempt to breed each year (Garðarsson & Skarphéðinsson 1984; Haapanen 1991; Rees et al. 1991; Einarsson 1996; Schadilov et al. 2002; Brazil 2003).

Non-breeders of most swan species gather in flocks and undergo wing moult near the breeding grounds (Brazil 2003). However, Whooper Swans in the Baltic region do not fit this general pattern. No mass-moulting sites have been located in Fennoscandia; only groups of local birds numbering up to 18 individuals in large mire complexes have been recorded (Haapanen 1991; Kampe-Persson et al. 2012). Likewise in the Baltic States, in 2012 only 187 moulting Whooper Swans were counted (Kampe-Persson et al. 2012). These groups represent a tiny proportion of all nonbreeding birds, given that the numbers breeding in Sweden and Finland now exceeds 10,000 pairs (Väisänen et al. 2011; Ottosson et al. 2012). It is hypothesised that the

Fennoscandian birds moult in highly productive wetlands in Russia, most likely in the Arkhangelsk Region (Boiko & Kampe-Persson 2012). Evidence for this has been lacking to date, however, although one bird colour-marked in Finland was observed moulting on the Kanin Peninsula (Litvin & Gurtovaya 2003) and three birds fitted with neck-collars in Latvia were found moulting in the Arkhangelsk Region (Boiko & Kampe-Persson 2012; Kampe-Persson *et al.* 2012).

The geographical affinities of migratory waterfowl and the exchange between flyways is usually quantified based on ring reencounters (Mooij 1997; Ely et al. 2014; Madsen et al. 2014), isotopic signatures (Fox et al. 2007; van Dijk et al. 2014) or genetic data (Butkauskas et al. 2012; Ely et al. 2017). Ringing and isotopic data can shed light on short-term exchanges, whereas genetic data usually only detect more permanent immigrations that led to gene flow. Although these are all useful methods for determining the extent of exchange between flyways, they at most provide coarse information about when and where such exchanges happen.

By equipping birds with tracking devices, a rapidly increasing amount of data are being gathered on migration routes (Kays *et al.* 2015). Such data have also recently been used to study migratory connectivity (Ely *et al.* 2014; Trierweiler *et al.* 2014). When birds from adjacent flyways are followed, their tracks might indicate areas of flyway overlap, which may be those areas where exchanges potentially take place. As tracking devices are costly, sample size often prevents the observation of actual exchange events, but the data derived are less prone to bias than ringing data, for which reporting rates may vary spatially (Korner-Nievergelt *et al.* 2010).

Methods

From 26–28 July 2016, ten cygnets, comprising eight females and two males, from seven different families, were fitted with solar GPS-GSM loggers in western Latvia (Table 1). Cygnets were caught for ringing at the age of 10–11 weeks, which in Latvia they reach from the middle of July to early August. At this age they were large enough to wear a neck-collar, but were still flightless.

We used solar-powered GPS-GSM-loggers developed by the University of Konstanz and the Max Planck Institute for Ornithology in Radolfzell, Germany. They had a mass of 20 g and their dimensions were $40 \times 26 \times 15$ mm. The devices were mounted vertically on conventional blue-coloured Whooper Swan neck-collars.

Dimensions and weight of the collars were: height 83 mm, inner diameter 57 mm, thickness of the plastic 3 mm and weight 71 g. The total mass of each collar fitted with a logger therefore was 91 g, which represented between 1.14–1.21% and 1.01– 1.57% of the total body mass of the males and females, respectively, in our study. Each collar had a white alphanumerical code of four digits which, during normal field conditions, were readable at a distance of 50–300 m using a 20–60× telescope.

The loggers were set to collect GPS coordinates every 15 min as a basic setting but in reality this rate was only achieved for very short periods. In the resulting dataset, intervals between successive GPS coordinates varied from 15 min to several weeks. This resulted from variation in onboard solar power availability and the ability of the tags to get valid GPS fixes.

Neck-collar Nr.	Sex	Ringing date	Ringing site	Last signal date	Country
9E01	female	28.07.2016	Poparāju pond, Alsunga	22.10.2017	Russia
9E02	female	26.07.2016	Renda 1, Kuldīga	23.08.2016	Latvia
9E03	female	28.07.2016	Poparāju pond, Alsunga	29.08.2019	Russia
9E04	female	26.07.2016	Renda 2, Kuldīga	27.09.2016	Latvia
9E05	female	26.07.2016	Rimzāti 4, Kuldīga	06.09.2017	Russia
9E07	female	26.07.2016	Rimzāti 5, Kuldīga	29.06.2018	Russia
9E08	male	26.07.2016	Rimzāti 4, Kuldīga	01.07.2017	Russia
9E09	female	27.07.2016	Upeslejas, Kuldīga	29.11.2016	Latvia
9E10	female	27.07.2016	Upeslejas, Kuldīga	17.06.2017	Russia
3E00	male	28.07.2016	Piena pond, Kuldīga	02.10.2016	Latvia

 Table 1. Ringing/tagging dates, places and sex for 10 Whooper Swan cygnets marked in

 Latvia, together with the country and date of the last GPS fix.

Once per day the loggers sent the stored GPS data via GSM (mobile data network) to the database www.movebank.org where all data were stored. In cases of bad or missing GSM connectivity the data were stored on the loggers and sent on subsequent occasions whenever GSM conditions were more favourable.

Pre-moult, moult and post-moult periods were defined as 1 May–28 June, 29 June–14 September and 15 September–31 October, respectively (Boiko & Kampe-Persson 2012).

Results

The GSM updates ceased for four out of the 10 birds in the autumn of 2016 (Table 1), which was to be expected considering that first-year mortality can reach 40% for Whooper Swan cygnets (Brazil 1983; Boiko 2008) and logger failure may also occur. Data for the other six birds are given below (see also Fig. 1). Here we only report on the pre-moult, moult and post-moult periods, without describing the stopover areas. Distances from the hatching to moulting sites is only given for birds where the precise location of the moulting site was known.

9E01 female

This bird left Latvia during the pre-moult period on 25 May 2017. It arrived at its moulting ground on 09 June 2017, in the area around Lake Vigozero (63.63°N, 34.65°E) in the Republic of Karelia, Russia. After the signal was lost there was no additional information about this bird. The



Figure 1. Moulting sites of Latvian Whooper Swans tagged with GPS-GSM transmitters in summer 2006. Triangles = moulting sites for 2nd year birds (n = 4); circles = moulting sites for 3rd year birds (n = 2); this information was derived from four individuals in total of 10 tagged, with a further two individuals supplying incomplete information about possible moulting sites not shown here. Approximate catch location is shown with a star.

straight-line distance from its hatching site was 1,038 km. The last signal was received on 22 October 2017.

9E03 female

This bird left Latvia during the pre-moult period on 25 May 2017. It arrived at the moulting ground on 3 July 2017 and left it again on 2 October 2017. In the summer of 2017, this bird moulted northeast of Kelmin Nos (68.06°N, 53.06°E) in the delta of the Pechora Rivera, Nenets Autonomous Okrug in the Arkhangelsk Region of Russia. The straight-line distance from its hatching site was 2,008 km.

In 2018 the same bird left Latvia in the pre-moult period on 27 May 2018. It arrived at the moulting ground on 25 May 2018 and left it again on 19 October 2018. In the summer of 2018, this bird moulted in wetlands 87 km southwest of Karatayka (68.16°N, 59.55°E), in the Nenets Autonomous Okrug within the Arkhangelsk Region of Russia. The straight-line distance from its hatching site to the 2018 moulting site was 2,489 km. The straight-line distance between the moulting grounds used in 2017 and 2018 was 309 km, with 9E03 moulting further east in 2018.

In 2019 the bird left Latvia in the premoult period on 18 May 2019. It arrived at the moulting ground (68.21°N, 59.24°E), 75 km to the west of its 2018 moulting site, on 25 June 2019. The last signal was received on 28 May 2019.

9E05 female

This bird left Latvia during the pre-moult period on 20 May 2017 and arrived at its possible moulting ground on 5 June 2017.

The last signal was taken on 6 September 2017. The exact moulting location therefore is not known, due to the lack of GPS fixes during the moult period, but it is most likely in the western part of the White Sea, north of Belomorsk, in the Republic of Karelia, Russia.

9E07 female

This bird left Latvia during the pre-moult period on 20 May 2017, arrived at the moulting ground on 25 June 2017, and left it again on 26 September 2017, having moulted south of Karatayka at (67.58°N, 61.13°E) in the Nenets Autonomous Okrug, within the Arkhangelsk Region of Russia. The straight-line distance from its hatching site was 2,524 km.

In 2018 this bird left Latvia during the pre-moult period on 21 May 2018. It arrived at the moulting ground on 21 June 2018. In the summer of 2018, this bird moulted in the Pechora River delta (67.55°N, 53.30°E), in the Nenets Autonomous Okrug of the the Arkhangelsk Region, Russia. The straight-line distance from its hatching site was 2,179 km. The straight-line distance between moulting grounds of the years 2017 and 2018 was 356 km (westerly direction). The last signal was received on 29 June 2018. However between 16 December 2018 and 21 March 2019, reports and photographs of this bird with an intact neck-collar but without the transmitter were received from observers in Germany and Latvia.

9E08 male

This bird left Latvia during the pre-moult period on 20 May 2017. It arrived at the moulting ground on 1 July 2017. In the summer of 2017 it moulted north of Nizhnyaya Pesha (66.46°N, 47.46°E) in the Nenets Autonomous Okrug within the Arkhangelsk Region of Russia. The last signal was received on 1 July 2017. The straight-line distance from the hatching site was 1,885 km.

Swan 9E08 was known to be still alive in May 2018, when its neck-collar was reported from Poland during winter 2017/ 2018, followed by reports from Latvia in spring 2018. The transmitter was still in place at that time, but no signals were being received.

9E10 female

This bird left Latvia during the pre-moult period on 25 May 2017. The last signal was received on 17 June 2017, during the time of pre-moult migration, in the vicinity of Yaringa village (64.52°N, 37.49°E), near Dvinsky Bay on the White Sea in the Arkhangelsk Region of Russia.

Migration distances and routes for all individuals during moult migration

The average straight-line distance between the moulting sites used by the tracked birds, from east to west, was 1,451 km. The shortest distance between hatching and moulting sites was 1,038 km and the longest was 2,524 km. The directional vector all birds took (*i.e.* the four birds, including two with repeat migrations and two further birds with less complete information) when heading towards moulting sites from the breeding areas was to the northeast. The average distance from the hatching sites to the moulting grounds was 1,864 km for the 2nd year birds (n = 4) and 2,334 km for the 3rd year birds (n = 2).

Discussion

During wing moult, waterfowl shed all of their flight feathers simultaneously, and cannot fly for some weeks until the flight feathers have regrown (Salomonsen 1968). Waterfowl are precocial and nidifugous species, meaning that their young are mobile and leave the nest shortly after hatching, weeks before they can fly. During this period, the young are accompanied by their parents, which also cannot fly at that time as they undergo wing moult soon after breeding. So, only birds that refrain from breeding or that fail in their breeding attempt are free to fly greater distances to moulting areas (Cramp & Simmons 1977; Jehl 1990; Aarvak & Øien 2003; Boiko & Kampe-Persson 2012). In our study, moult migrations were up to 2,524 km long. It is generally thought that such moult migrations take the birds to areas that are relatively safe and offer good feeding opportunities (Rees et al. 1997; Brazil 2003).

In a population model of the Whooper Swan in Finland, the annual growth rate was estimated at 11% and the percentage of non-breeders in summer at 70% (Haapanen 1991). The latter figure is similar to observations of > 60% of Whooper Swans in Iceland congregating in nonbreeding flocks in summer (Garðarsson & Skarphéðinsson 1984; Rees et al. 1991; Einarsson 1996) and 56-73% of Whooper Swans on the Pechora Delta remaining in non-breeding flocks in summer (Schadilov et al. 2002). As the annual growth rate for Whooper Swans in Latvia averaged 11% during the years 1980-2009 (Boiko & Kampe-Persson 2010), the Finnish model

might be used to estimate the number of non-breeders in the Latvian population. Such a calculation gives an increase in the number of non-breeders from about 750 in 2005 to about 1.200 in 2009. As there never were more than 85 moulters in total at the three moulting sites in Latvia, despite extensive surveys (Boiko 2008), and 187 in the Baltic States in 2012, these sites were hosting only a tiny fraction of all the potential moulting non-breeders. The vast majority of the birds that left presumably moulted in Russia. Of the neck-collared Whooper Swan cygnets hatched in Latvia, and known to be alive at the beginning of the moulting season, very few birds moulted in the Baltic States; only 1.1% (n = 351) and 1.3% (*n* = 521) in their 2nd and 3rd-6th calendar year, respectively. About 99% of the swans that hatched in Latvia left the country to moult elsewhere (Kampe-Persson et al. 2012).

None of the Leningrad, Pskov and Novgorod regions, nor the Republic of Karelia, had any known moulting sites for Whooper Swans at the start of the 21st century (Hoklova & Artemjev 2002). However, it remains possible that moult sites of minor importance exist in these parts of Russia as our study showed that at least one bird moulted in the vicinity of Lake Vigozero in the Republic of Karelia, with another possibly moulting in the western part of White Sea, north of Belomorsk, in the Republic of Karelia. In earlier years, a total of 1,510 Whooper Swans were found during aerial surveys of the Murmansk Region in 1975-1977, but the reports mention only breeding birds and say nothing about moulting (Bianki 1981; Bianki

& Shutova 1987). Waterfowl counts along the eastern coast of the Kola Peninsula in 1978–1979 revealed a total of 24 moulting Whooper Swans in June (Filchagov & Tserenkov 1984). The number of moulting non-breeders may however have been larger than this at that time, because Brazil (2003) stated that non-breeders arrived at moulting sites on the Kola Peninsula mainly in June.

In an area west of the River Mezen and Mezenskaya Bay, where two of the Latvian birds were found moulting in our previus study (Boiko & Kampe-Persson 2012), 420 Whooper Swans were counted during an aerial survey in 1975-1977 (Bianki & Shutova 1987). During the same survey 880 swans, probably Whooper Swans, were found east of River Mezen and around Cheshskava Bay. However, it remains unknown whether all of these birds were moulting. One of our study birds (this study) moulted north of Nizhnyaya Pesha in the Nenets Autonomous Okrug in the Arkhangelsk Region. Aerial surveys during the years 1973-1983 in the Nenets Autonomous Okrug revealed moulting flocks numbering 20-150 swans along the coast, in coastal lowlands and lowlands of tundra rivers (Mineev 1986). Unfortunately, there were no efforts to differentiate between Whooper and Bewick's Swans during these surveys. The same applies to the aerial survey made in 1975-1977, when a total of 7,600 swans were found east of Cheshskaya Bay (Bianki & Zhutova 1987). Little has been reported on the number of Whooper Swans moulting in the Malozemelskaya tundra and the Pechora River delta, but the Whooper Swan does not regularly moult on the Russky Zavorot

Peninsula, Kolokolkovskaya Bay and Korovinskaya Bay, which are to the north of the Pechora River delta (Mineev 2005).

Two of our study birds moulted at Khaypudyrskaya Bay in the Nenets Autonomous Okrug; one as a 2nd year bird and one as a 3rd year bird. Interestingly, both birds changed their moulting sites to/ from the Pechora River delta, where one bird moulted in its 2nd year and one in its 3rd year of life.

Although the picture of the movements of Latvian Whooper Swans is incomplete, it is safe to state that a majority of all nonbreeding Latvian Whooper Swans undergo a migration of > 1,000 km to reach their moulting grounds. The same very likely applies to all Whooper Swans around the Baltic Sea, even though birds from northerly breeding grounds have a shorter distance to cover. The four birds found moulting in Russia during this study might have given a slightly skewed picture however, because several studies have found differences between 2nd calendar year and older birds in the choice of moulting site (Mineev 1986; Mineev 2005; Degen & Heinicke 2007). A 4th calendar year bird shot in the Tuymen Region, east of the Ural Mountains in September 2010 might be an indication that older birds moult farther east than 2nd calendar year individuals (Boiko & Kampe-Persson 2012). However, it cannot be ruled out that this individual was dispersing. Lengthy moult migrations, usually northwards, are a widespread phenomenon in goose populations (Owen 1980). Among swans, on the other hand, most non-breeders undergo wing moult near the breeding grounds, and moult migration has only been described for the Mute Swan so far (Salomonsen 1968).

Traditional ringing has sometimes proven inefficient in mapping the occurrence of a species, except in areas where animals are hunted, with either shotgun, net or camera (Csörgö *et al.* 2009). The same applies to neck-collaring when birds occur in inaccessible and sparsely populated areas. Thus, even though we only have six records of Whooper Swans fitted with data loggers, this report provides a first indication of moult migration in Latvian Whooper Swans.

Telemetry has become a valuable tool for mapping migration routes as well as sites for stopover, wintering and moulting. Moreover, this study was not the first one to find moulting sites of a Red-listed waterfowl species in Russia. Lesser White-fronted Geese Anser erythropus marked on a staging area in northern Norway were found moulting on the Taimyr Peninsula (Aarvak & Øien 2003; Øien et al. 2009) and Taiga Bean Geese Anser fabalis fabalis marked on spring-staging areas in northern Sweden were found moulting on Novaya Zemlya (Nilsson et al. 2010). To be efficient, however, this technique has to be combined with fieldwork in the mapped areas. For small populations field surveys are the obvious choice. For that reason, an autumn staging site of the Fennoscandian Lesser White-fronted Goose, located on the Kanin Peninsula in 1995 (Lorentsen et al. 1998), was visited by field teams in 1996 and 2008 (Tolvanen 1998; Tolvanen et al. 2009). Field surveys are also important for large populations, especially to obtain data about habitat use, food choice, local movement patterns, conservation threats, and other

relevant information. However, to become efficient for large populations occurring in inaccessible and sparsely populated areas, remote telemetry and field studies must be combined with aerial surveys. It is particularly applicable in the case of the Whooper Swan, because the efficiency of aerial surveys for that species has proven to be high (Haapanen & Nilsson 1979). As there are good reasons to assume that the main moulting grounds for Whooper Swans from all countries around the Baltic Sea are situated in the Arkhangelsk Region, there ought to be sufficient interest in organising aerial surveys of the aforementioned areas.

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References

- Aarvak, T. & Øien, I.J. 2003. Moult and autumn migration of non-breeding Fennoscandian Lesser White-fronted Geese *Anser erythropus* mapped by satellite telemetry. *Bird Conservation International* 13: 213–226.
- Bianki, V.V. 1981. Swans and geese in Murmansk Region and northern Karelia. In G.V.T. Matthews & Yu.A. Isakov (eds.), Proceedings of the Symposium on the Mapping of Waterfowl Distributions, Migrations and Habitats. Alushta, Crimea, USSR, November 1976, pp. 225– 231. All-Union Research Institute of Nature Conservation and Nature Reserve

Management, USSR Ministry of Agrigulture, Institute of Geography, USSR Academy of Sciences, Moscow, Russia.

- Bianki, V.V. & Shutova, E.V. 1987. Distribution and numbers of swans in the northern part of European USSR. *In* E.V. Syroechkovski (ed.), *Ecology and Migration of Swans in the* USSR, pp. 20–28. Nauka, Moscow, Russia. [In Russian.]
- Boiko, D. 2008. Territorial and temporal distribution of Whooper Swan *Cygnus cygnus* marked with neck collars in Latvia in 2003– 2005. *Acta Universitatis Latviensis, Biology* 745: 53–61.
- Boiko, D. & Kampe-Persson, H. 2010. Breeding Whooper Swans *Cygnus cygnus* in Latvia, 1973–2010. *Wildfowl* 60: 168–177.
- Boiko, D. & Kampe-Persson, H. 2012. Moult migration of Latvian whooper swans *Cygnus cygnus*. Ornis Fennica 89: 273–280.
- Brazil, M. 1983. Preliminary results from a study of Whooper Swan movements using neckcollars. *Journal of the College of Dairying* 10: 79–90
- Brazil, M. 2003. *The Whooper Swan*. T. & A.D. Poyser, London, UK.
- Butkauskas, D., Švažas, S., Tubelyt, V., Morkūnas, J., Sruoga, A., Boiko, D., Paulauskas, A., Stanevičius, V. & Baublys, V. 2012. Coexistence and population genetic structure of the whooper swan *Cygnus cygnus* and mute swan *Cygnus olor* in Lithuania and Latvia. *Central European Journal of Biology* 7: 886–894.
- Cramp, S. & Simmons, K.E.L. (eds.). 1977. The Birds of the Western Palearctic, Vol. 1. Oxford University Press, Oxford, UK.
- Csörgö, T., Karcza, Z., Halmos, G., Magyar, G., Gyurácz, J., Szép, T., Bankovics, A., Schmidt, A. & Schmidt, E. (eds.). 2009. *Hungarian Bird Migration Atlas*. Kossuth Kiadó, Budapest, Hungary. [In Hungarian with English summary.]
- Degen, A. & Heinicke, T. 2007. Whooper Swan Cygnus cygnus. In T. Heinicke & U. Köppen

(eds.), *Bird Migration in East Germany* – *Waterbirds Part* 1, pp. 44–56. (Berichte Vogelwarte Hiddensee, Greifswald, Germany. [In German with English summary.]

- Dement'ev, G.P. 1935. Birds in the Kanin Peninsula. Collection of Works of the Zoological Museum 2: 23–55. [In Russian.]
- van Dijk, J.G.B., Meissner, W. & Klaassen, M. 2014. Improving provenance studies in migratory birds when using feather hydrogen stable isotopes. *Journal of Avian Biology* 45: 103–108.
- Einarsson, Ó. 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. Ph.D. thesis, University of Bristol, Bristol, UK.
- Ely, C.R., Sladen, W.J.L., Wilson, H.M., Savage, S.E., Sowl, K.M., Henry, B., Schwitters, M. & Snowdon, J. 2014. Delineation of tundra swan *Cygnus c. columbianus* populations in North America: geographic boundaries and interchange. *Wildfowl* 64: 132–147.
- Ely, C.R., Wilson, R.E. & Talbot, S.L. 2017. Genetic structure among greater whitefronted goose populations of the Pacific flyway. *Ecology and Evolution* 7: 2956–2968.
- Filchagov, A.V. & Tserenkov, A.E. 1984. Waterfowl numbers at the eastern coast of the Kola Peninsula. Ornithologija 12: 215–216. [In Russian.]
- Fox, A.D., Christensen, T.K., Bearhop, S. & Newton, J. 2007. Using stable isotope analysis of multiple feather tracts to identify moulting provenance of vagrant birds: a case study of Baikal teal *Anas formosa* in Denmark. *Ibis* 149: 622–625.
- Garðarsson, A. & Skarphéðinsson, K.H. 1984. A census of the Icelandic Whooper Swan population. *Wildfowl* 35: 37–47.
- Haapanen, A. 1991. Whooper Swan Cygnus c. cygnus population dynamics in Finland. In

J. Sears & P.J. Bacon (eds.), *Proceedings of the Third IWRB International Swan Symposium*, *Oxford 1989. Wildfowl* (Supplement No. 1): 137–141.

- Haapanen, A. & Nilsson, L. 1979. Breeding waterfowl populations in northern Fennoscandia. Ornis Scandinavica 10: 145–219.
- Hoklova, T.Y. & Artemyev, A.V. 2002. Reassessment of the Southern Limit for Whooper Swans Breeding in Northwest Russia. *Waterbirds* 25 (Special Publication 1): 67–73.
- Jehl Jr., J.R. 1990. Aspects of the molt migration. In E. Gwinner (ed.), Bird Migration: Physiology and Ecophysiology, pp. 102–113. Springer-Verlag, Berlin, Germany.
- Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. 2015. Terrestrial animal tracking as an eye on life and planet. *Science* 348: aaa2478.
- Kampe-Persson, H., Boiko, D. & Morkūnas, 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.
- Korner-Nievergelt, F., Sauter, A., Atkinson, P.W., Guélat, J., Kania, W., Kéry, M., Köppen, U., Robinson, R.A., Schaub, M., Thorup, K., van der Jeugd, H. & van Noordwijk, A.J. 2010. Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity. *Journal* of Avian Biology 41: 8–17.
- Lammi, E. 1983. Laulujoutsen Cygnus cygnus. In K. Hyytiä, E. Kellomäki & J. Koistinen (eds.), Suomen Lintuatlas, pp. 30–31. SLY:n Lintuteito Oy, Helsinki, Finland. [In Finnish.]
- Litvin, K. & Gurtovaya, E.N. 2003. Moult migration of the Whooper Swan at the Kanin Peninsula. In V.B. Zimin, A.B. Popovkina & E.E. Syroechkovski, Jr. (eds.), Management and Conservation of Waterfowl populations in Northern Eurasia (with Special Focus on the White Sea – Baltic Flyway): Abstracts, presented to the

International Symposium April 2003, Olonets, Karelia, Russia, pp. 106–107. Goose, Swan and Duck Study Group of Northern Eurasia & Karelian Research Centre of Russian Academy of Science, Petrozavodsk, Russia. [In Russian.]

- Lorentsen, S.-H., Øien, I.J. & Aarvak, T. 1998. Migration of Fennoscandian Lesser Whitefronted Geese *Anser erythropus* mapped by satellite telemetry. *Biological Conservation* 84: 47–52.
- Madsen, J., Tjørnløv, R.S., Frederiksen, M., Mitchell, C., Sigfússon, A.T. & Pärt, T. 2014. Connectivity between flyway populations of waterbirds: assessment of rates of exchange, their causes and consequences. *Journal of Applied Ecology* 51: 183–193.
- Mineev, Yu. N. 1986. Seasonal distribution and the numbers of swans in the north-east of the European part of the USSR. Bulletin of the Moscow Society of Nature Explorers, Department of Biology 91: 19–27. [In Russian with English summary.]
- Mineev, O. Yu. 2005. Waterfowl of Malozemelskaya Tundra and Pechora River Delta. Ural Division of Russian Academy of Science, Yekaterinburg, Russia. [In Russian.]
- Mooij, J.H. 1997. The status of White-fronted Goose (*Anser A. albifrons*) in the Western Palearctic. *Vogelwarte* 39: 61–81.
- Nilsson, L., de Jong, A., Heinicke, T. & Sjöberg, K. 2010. Satellite tracking of Bean Geese *Anser fabalis fabalis* and *A.f.rossicus* from spring staging areas in northern Sweden to breeding and moulting areas. *Ornis Svecica* 20: 184–189.
- Øien, I.J., Aarvak, T., Ekker, M. & Tolvanen, P. 2009. Mapping of migration routes of the Fennoscandian Lesser White-fronted Goose breeding population with profound implications for conservation priorities. *In P.* Tolvanen, I.J. Øien & K. Ruokolainen (eds.), *Conservation of Lesser White-fronted Goose on the*

European migration route. Final report of the EU LIFE-Nature project 2005–2009, pp. 12–18. WWF Finland Report No. 27 & NOF Rapportserie Report No. 1-2009. World Wildlife Fund, Helsinki, Finland & Norwegian Ornithological Society, Trondheim, Norway.

- Ottosson, U., Ottvall, R., Elmberg, J., Green, M., Gustafsson, R., Haas, F., Holmqvist, N., Lindström, Å., Nilsson, L., Svensson, M., Svensson, S. & Tjernberg, M. 2012. Fåglarna i Sverige – Antal och Utbredning. Sveriges Ornitologiska Förening, Stockholm, Sweden. [In Swedish with English summary.]
- Owen, M. 1980. *Wild Geese of the World.* B.T. Batsford, London, 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.
- Rees, E., Einarsson, Ó. & Laubek, B. 1997. Cygnus cygnus Whooper Swan. BWP Update 1: 27–35.
- Salomonsen, F. 1968. The moult migration. *Wildfowl* 19: 5–24.
- Schadilov, Yu. 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.
- Svensson, S., Svensson, M. & Tjernberg, M. 1999. Svensk Fågelatlas. Vår Fågelvärld, Supplement No. 31. Sveriges Ornitologiska Förening, Stockholm, Sweden. [In Swedish.]
- Tolvanen, P. 1998. Lesser White-fronted Goose Anser erythropus expedition to the Kanin Peninsula in 26 August–12 September, 1996, and the establishment of the Shoininsky Reserve. In P. Tolvanen, K. Ruokolainen, J. Markkola & R. Karvonen (eds.), Finnish Lesser White-fronted Goose Conservation Project. Annual Report 1997, pp. 33–35. WWF Finland

Report No. 9. World Wildlife Fund Finland, Helsinki, Finland.

- Tolvanen, P., Aarvak, T. & Anufriev, V. 2009.
 Lesser White-fronted Goose survey on Kanin Peninsula, Russia, in September 2008.
 In P. Tolvanen, I.J. Øien & K. Ruokolainen (eds.), Conservation of Lesser White-fronted Goose on the European Migration Route. Final Report of the EU LIFE-Nature project 2005–2009, pp. 40–43. WWF Finland Report No. 27 & NOF Rapportserie Report No. 1-2009.
 World Wildlife Fund, Helsinki, Finland & Norwegian Ornithological Society, Trondheim, Norway.
- Trierweiler, C., Klaassen, R.H.G., Drent, R.H., Exo, K.M., Komdeur, J., Bairlein, F. & Koks, B.J. 2014. Migratory connectivity and population-specific migration routes in a longdistance migratory bird. *Proceedings of the Royal Society B-Biological Sciences* 281: 20132897.
- Väisänen, R.A., Hario, M. & Saurola, P. 2011. Population estimates of Finnish birds. In J. Valkama, V. Vepsäläinen & A. Lehikoinen (eds.), The Third Finnish Breeding Bird Atlas. Finnish Museum of Natural History & Ministry of Environment, Helsinki, Finland. Available at http://atlas3.lintuatlas.fi/results/ specieslist (last accessed 27 October 2019).



Photograph: Whooper Swans on migration through Russia, by Ben Cherry.



Photograph: Whooper Swan adult in flight in Hokkaido, Japan, by Dickie Duckett/FLPA.



Photograph: Whooper Swan adults and juveniles on water in Norway, December 2010, by Erlend Haarberg/NPL.

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