GPS-tracked migrations of Icelandic Whooper Swans *Cygnus cygnus* to mainland Europe and a case of repeated flyway interchange

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Abstract

Interchange between biogeographically discrete flyways of long-distance migrants redistributes individuals across wintering systems, affecting gene flow and our understanding of population trajectories. However, the ecological mechanisms and frequency of such movements remain largely unknown. The Iceland (breeding) population of Whooper Swans *Cygnus cygnus* spend the summer in Iceland and winters predominantly in Britain and Ireland, although small numbers of colour-marked individuals have previously been recorded overwintering on mainland Europe. Of 56 Whooper Swans GPS-tagged in Iceland in 2024, 46 migrated south for the 2024/25 winter, and two of these crossed the North Sea to Friesland and Zeeland in the Netherlands. Their 2,178–2,344 km autumn migrations involved extensive oversea flights and prolonged staging within Britain before continuing to the Netherlands in mid–late November. Both subsequently completed return migrations to Iceland in spring, including one direct 1,861 km transoceanic crossing

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between the Netherlands and Iceland, completed in 84 h. One individual migrated to the same Dutch region the following winter, confirming repeated use of wintering areas within the wintering range of the North Mainland Europe (breeding) population of Whooper Swans (NME) flyway. In the Netherlands, both birds occupied winter home ranges (95% KUD = 1,575–2,768 ha) centred on agricultural feeding areas and nearby wetland roost sites. Updated analysis of colour-ring observations further supported Iceland–Netherlands connectivity, with 25 Icelandic-ringed Whooper Swans from across the breeding range recorded in the Netherlands, mostly from Friesland. These tracking data are the first detailed description of the swans' movements from Iceland to mainland Europe, highlighting the potential for increasing interchange between the Icelandic and Northwest Mainland European flyways.

Key words: flyway interchange, GPS tracking, migration ecology, migratory routes, Whooper Swan.

The Iceland (breeding) Whooper Swan *Cygnus cygnus* population (formerly the Iceland, UK/Ireland population), which was estimated at 43,255 individuals in 2020, breeds almost exclusively in Iceland and migrates to winter mainly in Britain and Ireland (Rees & Clausen 2024; Brides *et al.* 2021; Burke *et al.* 2021). Around 2,000–3,000 individuals remain in Iceland each year (Brides *et al.* 2021), and 272–520 birds were thought to winter on mainland Europe during the 2020 and 2025 population censuses (Brides *et al.* 2022). Both the Iceland (breeding) (hereafter Icelandic) and North Mainland European (breeding) Whooper Swan populations (formerly the Northwest Mainland European population, hereafter NME) have increased markedly in recent decades, resulting in more birds using the migratory systems (flyways) linking their respective breeding and wintering grounds. Migrations by the NME population (recently put at > 140,000 birds; Rees & Clausen 2024) are facilitated by the birds being able to make short "stepping-stone" flights across a continuous landmass, avoiding major sea crossings. By contrast, movement of Icelandic swans to mainland Europe requires a longer migration than for those wintering in Britain and Ireland and additional North Sea crossings, increasing energy demands and risk exposure (*e.g.* if encountering adverse weather during the crossings), with possible consequences for survival and fitness.

Changes in winter distribution have important implications for flyway delineation and population assessment. Even limited interchange between the Icelandic and NME flyways can complicate the assignment of individuals to breeding populations and migration routes, increasing uncertainty in abundance estimates for both populations. Although colour-marking studies have shown that small numbers of Icelandic-ringed Whooper Swans overwinter on mainland Europe, including individuals showing multi-year site fidelity (Brides *et al.* 2022), key aspects of their migration ecology – such as migratory routes, staging

areas, habitat use and migratory timing – remain poorly understood.

GPS tracking offers a means for quantifying such movements (Brides *et al.* 2022). Detailed routes and timing data are essential to monitor population interchange, identify environmental or demographic drivers and maintain robust flyway-level population assessments for Europe's rapidly growing Whooper Swan populations. Beyond informing population monitoring, management and policy, such data also improve our understanding of migration ecology by revealing behavioural plasticity and how migratory species exploit new wintering opportunities in response to environmental change.

The Netherlands lies on the southwestern periphery of the NME wintering range, typically supporting < 2,500 individuals (1.7% of the NME population in 2015; Laubek *et al.* 2019), although sometimes increasing to levels of *c.* 4,000 individuals during periods of severe frost and heavy snowfall (Hornman *et al.* 2025). While most Dutch-wintering birds originate from the NME population, ring resightings confirm a small but increasing number of Icelandic colour-marked Whooper Swans, mainly in northern Friesland (Brides *et al.* 2022).

Satellite and GPS-GSM tags have been used to track Icelandic Whooper Swan migration since the 1990s but none of the previous studies recorded movements to mainland Europe (Pennycuick *et al.* 1996, 1999; Griffin *et al.* 2010, 2011). A new GPS-GSM tracking study, which commenced in August 2024 (during which 56 Whooper Swans were tagged, however provided an opportunity to tag an individual known from a previous resighting to have wintered in the Netherlands, together with a second swan of previously unknown wintering origin, both of which subsequently migrated to the Netherlands. Here we therefore present the first GPS-tracked routes, timing and staging behaviour of Whooper Swans migrating between Iceland and mainland Europe, placing these movements in the context of the wider GPS-tagged cohort wintering in Britain and Ireland. We also analyse winter home-range use in the Netherlands and use updated colour-ring resightings to assess Iceland–Netherlands connectivity, to determine whether swans wintering in the Netherlands originate from different parts of the Icelandic breeding range.

Methods

Capture and GPS-tagging

Whooper Swans were caught in August 2024 at nine wetland locations in the Fljótsheiði area of northern Iceland, where ringing has taken place since the 1980s (Newth *et al.* 2007). All GPS-tagged birds were equipped with GPS-GSM neck-collar tracking devices, either Ornitela OT-N55-3GC-C20 (n = 11) or Druid FLEX GPS-GSM (n = 45). Ornitela devices were programmed to obtain frequent GPS fixes, with the median interval of 10 min, whereas Druid FLEX devices typically recorded hourly fixes (median interval = 60 min), with occasional variation in fix frequency depending on battery conditions. No thinning of the higher-frequency Ornitela data was undertaken prior to analysis, and all available high-quality GPS fixes were retained. The capture, ringing and deployment of GPS-

GSM tags on the swans was undertaken under license from the National Science Institute of Iceland.

Two focal individuals (yellow leg ring codes AAF and ZTD, first marked in 2018 and 2022, respectively) were tagged at Kálfborgarárvatn (65.491°N, 17.319°W) and Kálfatjarnir (65.609°N, 17.441°W) on 6 and 9 August 2024, while flightless during the annual moult. AAF was fitted with an Ornitela OT-N55-3GC-C20 transmitter and ZTD with a Druid FLEX GPS-GSM transmitter. Birds were caught by hand from a small zodiac using a swan hook, placed in protective swan jackets, sexed by cloacal examination, marked with plastic and metal leg-rings (if unringed) and biometric data were recorded, following Newth *et al.* (2007).

In August 2025, AAF was recaptured at its breeding location with a damaged transmitter, which was replaced with a new GPS–GSM Interrex/Druid collar. The damage had occurred after arrival in Iceland, so spring 2025 migration data were unaffected.

Colour-marking and resighting data

To provide an updated assessment of interchange between the Icelandic and NME flyways following Brides *et al.* (2022), resighting records of Icelandic colour-marked Whooper Swans were extracted from long-term study databases. Birds were identified by their individually coded colour-rings, for which a comprehensive overview is provided by Brides *et al.* (2022). Resightings were contributed by researchers and birdwatchers throughout the flyways, with additional coordination in the Netherlands through a network of ring readers. For the present study, all records of Icelandic-marked Whooper Swans from the Provinces of Friesland and Zeeland in the Netherlands were collated and mapped to illustrate ringing origins and wintering locations.

Migration timing and distance

Migration timing and distance metrics were calculated for all GPS-tagged birds that completed migration, allowing the two focal individuals wintering in the Netherlands to be compared with the wider tagged cohort. Metrics were calculated for the 2024 and 2025 autumn migrations and the 2025 spring migration. Individuals that died, suffered transmitter failure or battery depletion before completing return migrations were excluded, as is standard in long-term telemetry studies, noting that annual survival estimates for adult Icelandic Whooper Swans range from 77–85% (Soriano-Redondo *et al.* 2023). Spring 2026 metrics were calculated only for AAF, as other tagged birds had yet to complete their migration. ZTD's tag ceased transmitting data on 5 June 2025, preventing further analysis.

Departure from Iceland was defined as the first GPS fix recorded over the sea after leaving land, identified through visual inspection of sequential GPS locations and mapped migration tracks. Completion of autumn migration was defined as arrival at the site or area where the bird subsequently spent the most days, and when directed southward or eastward movements (characteristic of migration) ceased, determined from visual inspection of the movements recorded. Completion of spring migration was defined as return to the Fljótsheiði area of Iceland or the area subsequently used for summering. In both

cases, migration completion was determined by visual inspection of the tracks.

Migration distance was calculated as the cumulative distance travelled between migration start and end points. For autumn migration this was defined as the location in Fljótsheiði or elsewhere in Iceland from which sustained migratory movement commenced and the location where the individual subsequently spent most of the winter period; *vice versa* for spring migration. Start and end points were again identified through visual inspection of sequential GPS locations and mapped migration tracks. Distances were calculated in QGIS (QGIS Development Team, 2024) by generating movement tracks from temporally ordered GPS fixes (using the "Points to Path" tool) and summing track lengths. Only fixes associated with directed migratory movements between staging sites were included; local movements within staging areas were excluded. Staging areas were defined as locations where individuals remained for a prolonged period and exhibited localised movements before resuming directional migration. Migratory phases were identified through visual inspection of movement tracks.

Wintering country was defined as the country in which an individual spent the greatest number of days between completion of autumn migration and initiation of spring migration.

Home range analyses

Home range analyses were conducted only for the two focal individuals wintering in the Netherlands, using R version 4.3.1 (R Core Team, 2023). Kernel utilisation distributions (KUDs) were estimated using the "*kernelUD*" function in the adehabitatHR package (Calenge & Fortmann-Roe 2023), with the "reference bandwidth" used as the smoothing parameter. The reference bandwidth (href) was selected because it provides a standardised and reproducible method for selection. Although href can over-smooth utilisation distributions, the same approach was applied consistently to all analyses to ensure comparability.

Analyses included all GPS fixes recorded between arrival in the Netherlands and departure on spring migration. For AAF, the first three locations after landfall in the Netherlands were excluded as short coastal post-migration resting movements, not subsequently revisited.

The dataset comprised 7,563 fixes (16 November 2024 to 7 March 2025) and 3,546 fixes (21 November 2025 to 16 March 2026) for AAF and 1,912 fixes (22 November 2024 to 8 March 2025) for ZTD. We estimated 95% home ranges and 50% core areas for all fixes and separately for daytime and nighttime, classified according to the sunrise and sunset times associated with each GPS fix using the "*getSunlightTimes*" function in the suncalc package (Thieurmel & Elmarhraoui 2023). Home range area was calculated using "*st_area*" in the sf package (Pebesma 2018).

Results

Capture, tagging & wintering locations

A total of 211 Whooper Swans were captured, of which 56 individuals (26.5%) were fitted with GPS-GSM neck collars. Of the tagged birds, 46 (82.1%) successfully completed migrations to wintering grounds

outside of Iceland in autumn 2024. By autumn 2025, only 20 transmitters remained functional owing to tag loss, transmitter malfunction and mortality, of which 12 individuals (21.4% of the originally tagged cohort) migrated to wintering grounds outside Iceland.

In winter 2024/25, 26 individuals (46.4%) spent the greatest number of days in England, 8 (14.3%) in the Republic of Ireland, 6 (10.7%) in Scotland, 2 (3.6%) in Northern Ireland, 2 (3.6%) in Wales, and 2 (3.6%) in the Netherlands (Fig. 1). Eight individuals (14.3%) remained in Iceland throughout the winter, while two transmitters (3.6%) ceased functioning prior to migration and no wintering destination could be assigned. A broadly similar distribution of wintering locations was observed in 2025/26, although fewer transmitters remained functional.

Migration timing

Migration timing of the two focal individuals was consistent with that observed for the wider tagged cohort. Across all

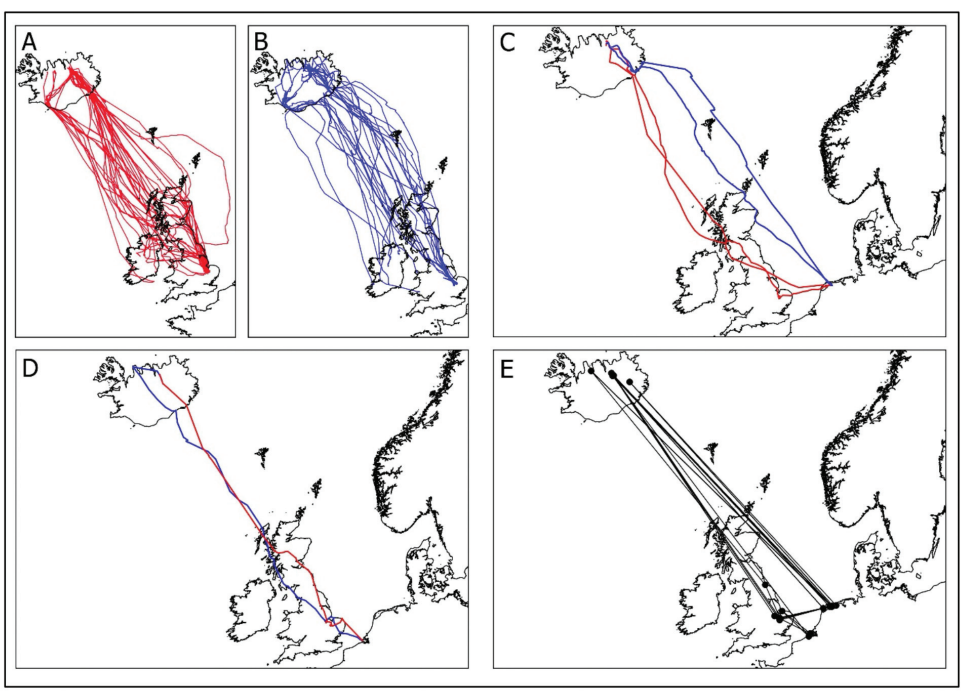


Figure 1. Migration routes and ringing locations of Icelandic Whooper Swans. (A) Autumn migration routes of non-focal GPS-tagged swans. (B) Spring migration routes of non-focal GPS-tagged swans. (C) Autumn (red) and spring (blue) migration tracks of focal individual AAF. (D) Autumn (red) and spring (blue) migration tracks of focal individual ZTD. (E) Ringing locations in Iceland and re-encounter locations of 20 colour-marked Whooper Swans recorded in the Friesland and Zeeland regions of the Netherlands. Re-encounters in the UK and Belgium are also shown.

tagged birds, autumn departure from Iceland in 2024 occurred between 23 September–17 November (mean = 11 October) (Table 1). The two focal individuals departed on 10 and 11 October 2024, respectively, both close to the cohort average.

In spring 2025, migration of the tagged cohort from Britain and Ireland commenced between 17 March–30 April (mean = 1 April). The two focal individuals departed their wintering areas in the Netherlands earlier, on 7 and 8 March 2025, and subsequently left the UK on 16 March and 1 April 2025, the latter falling within the cohort window.

In autumn 2025, departure from Iceland across the tagged cohort occurred between 4 October–15 December (mean = 24 October). The focal individual AAF departed Iceland on 11 November 2025, towards the later part of this period. Following wintering in the Netherlands, AAF subsequently departed on spring migration on 18 March 2026 and arrived back in Fljótsheiði, Iceland on 31 March 2026, taking a more or less direct flight without staging in the UK (see below).

Migration distance

Migration distances of the two focal individuals were consistently towards the upper end of those recorded within the wider tagged cohort. Across all tagged birds migrating from Iceland in autumn 2024, migration distances ranged from 1,234–2,405 km (mean ± s.d. = 1,919 ± 232 km, n = 36, 95% CI = 1,842–1,994). The focal individuals migrated 2,344 km (AAF) and 2,216 km (ZTD) to the Netherlands (Figs. 1C & 1D, Table 1). Spring 2025 migration distances ranged from 1,232–2,606 km (mean ± s.d. = 1,765 ± 308 km, n = 35, 95% CI = 1,683–1,882), with the return migration of ZTD (2,533 km) again towards the upper end of the cohort range (Fig. 1D, Table 2). During autumn 2025, migration distances ranged from 1,085–2,346 km (mean ± s.d. = 1,734 ± 344 km, n = 12, 95% CI = 1,539–1,928), with the focal individual AAF migrating 2,178 km via Britain to the Netherlands, also towards the upper end of the cohort range (Fig. 1C). In spring 2026, AAF migrated 2,075 km directly to Iceland, 89.7% of which was over sea (Fig. 1C, Table 2).

Autumn migration and staging of birds tracked to the Netherlands

Both focal individuals departed northern Iceland in early to mid-October 2024 and undertook multi-stage migrations involving extensive oversea movements and prolonged staging in Britain before continuing to the Netherlands (Figs. 1C & 1D, Table 1). Total autumn migration distances ranged from 2,216 to 2,344 km and took 35–42 days to complete. Oversea movements accounted for 48–56% of total migration distance in autumn 2024 (Table 1).

Following departure from Fljótsheiði, both individuals paused for only a few hours (< 4 h) at the important Whooper Swan staging wetland at Lón in eastern Iceland before initiating their first major sea crossing to Great Britain. After landfall in western Scotland, both birds moved to eastern England where they staged for several weeks, using a network of lowland wetlands and surrounding arable farmland. The Ouse Washes emerged as a particularly important staging site, with individuals remaining for 10–32 days prior to onward

Table 1. Autumn migration metrics for GPS-tagged Whooper Swans migrating from Iceland to Britain, Ireland and the Netherlands.

Bird	AAF	ZTD	All other tagged birds	AAF	All other tagged birds
Autumn (year)	**2024**	**2024**	**2024**	**2025**	**2025**
Departure to wintering grounds (date leaving Iceland)	10 Oct 2024	11 Oct 2024	Range: 23 Sept 2024–17 Nov 2024 Mean: 11 Oct 2024	11 Nov 2025	Range: 4 Oct 2025–15 Dec 2025 Mean: 24 Oct 2025
Arrival at final wintering area (in Britain, Ireland or the Netherlands)	15 Nov 2024	22 Nov 2024	Range: 28 Sept 2024–21 Dec 2024 Mean: 29 Oct 2024	20 Nov 2025	Range: 22 Oct 2025–3 Dec 2025 Mean: 4 Nov 2025
Total flight distance (km)	2,344	2,216	Range: 1,234–2,405 Mean (± s.d.): 1,919 (± 231.6) 95% CI: 1,842–1,994 (n = 36)	2,178	Range: 1,085–2,346 Mean (± s.d.): 1,734 (± 343.9) 95% CI: 1,539–1,928 (n = 12)
Distance over sea (km)	1,319	1,058	Range: 861–1,695 Mean (± s.d.): 1,224 (± 190.7) 95% CI: 1,175–1,290 (n = 36)	1,335	Range: 838–1,573 Mean (± s.d.): 1,150 (± 189.9) 95% CI: 1,079–1,278 (n = 12)
% over sea	56.3	48.0	Range: 47.1–85.0 Mean (± s.d.): 64.7 (± 9.02) 95% CI: 61.9–67.4	61.3	Range: 55.6–79.4 Mean (± s.d.): 67.3 (± 7.74) 95% CI: 63.0–71.7
Total duration of migration (days)	35	42	Range: 2–62 Mean (± s.d.): 17.1 (± 2.93) 95% CI: 11.8–22.8	9	Range: 1–42 Mean (± s.d.): 13.3 (± 16.0) 95% CI: 4.0–22.1

Table 2. Spring migration metrics for GPS-tagged Whooper Swans migrating from Britain, Ireland and the Netherlands to Iceland.

Bird	AAF	ZTD	All other tagged birds	AAF
Spring (year)	**2025**	**2025**	**2025**	**2026**
Departure from wintering grounds to Iceland	07 Mar 2025	08 Mar 2025	Range: 17 Mar 2025–30 Apr 2025 Mean: 1 Apr 2025	18 Mar 2026
Arrival at final summering area in Iceland	17 Mar 2025	03 Apr 2025	Range: 19 Mar 2025–11 June 2025 Mean: 11 Apr 2025	31 Mar 2026
Total flight distance (km)	2,064	2,533	Range: 1,232–2,606 Mean (± s.d.): 1,765 (± 307.5) 95% CI: 1,683–1,882 (n = 35)	2,075
Distance over sea (km)	1,800	1,109	Range: 870–1,410 Mean (± s.d.): 1,090 (± 146.4) 95% CI: 1,042–1,142 (n = 35)	1,861
% over sea	87.2	40.8	Range: 40.8–87.0 Mean (± s.d.): 62.7(± 12.08) 95% CI: 58.0–66.3	89.7
Total duration of migration (days)	9	26	Range: 1–69 Mean (± s.d.): 11.4 (± 15.57) 95% CI: 7.0–16.6	13

migration. In autumn 2025, AAF undertook a second migration to the same wintering region in the Netherlands, broadly following the route and strategy observed in autumn 2024, with extensive oversea movements interspersed with short staging periods in Great Britain before the final North Sea crossing (Fig. 1C, Table 1). The transmitter fitted to ZTD ceased transmitting in summer 2025, so its migration during winter 2025/26 could not be tracked. However, the bird was subsequently identified from its colour-ring in Belgium in January 2026.

Winter home range analyses

Upon arrival in the Netherlands, both individuals remained within restricted home ranges throughout the winter tracking period (Figs. 2 & 3, Table 3). The 95% kernel utilisation distribution (KUD) estimated from all fixes was 2,768 ha for ZTD during winter 2024/25, and 1,575 ha and 2,088 ha for AAF during winters 2024/25 and 2025/26, respectively. ZTD generally used the same areas during both day and night (resulting in similar home-range estimates for the two periods), whereas AAF showed

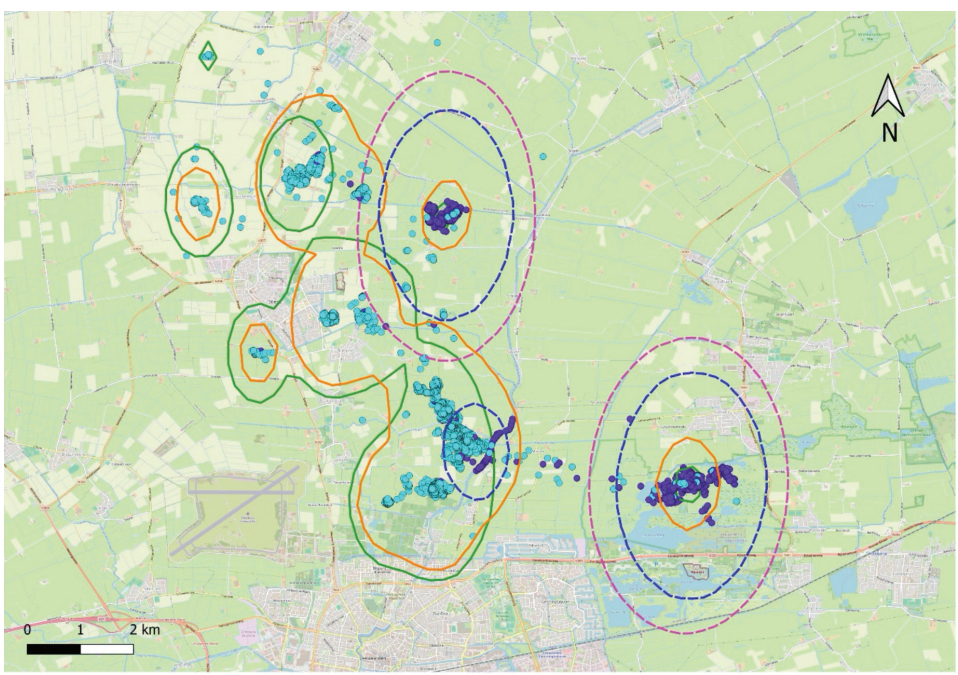


Figure 2. Home ranges of focal bird AAF in the Netherlands (north of Leeuwarden) estimated using the 95% Kernel Utilisation Distribution (KUD) method. The location of the study area within the Netherlands is shown in Fig. 1E. Light blue points represent winter 2024/25 daytime GPS fixes; dark blue points represent winter 2024/25 nighttime fixes. Orange solid polygons indicate the winter 2024/25 daytime home range, while green solid polygons indicate the winter 2025/26 daytime home range. Pink dashed polygons indicate the winter 2024/25 nighttime home range, while dark blue dashed polygons indicate the winter 2025/26 nighttime home range.

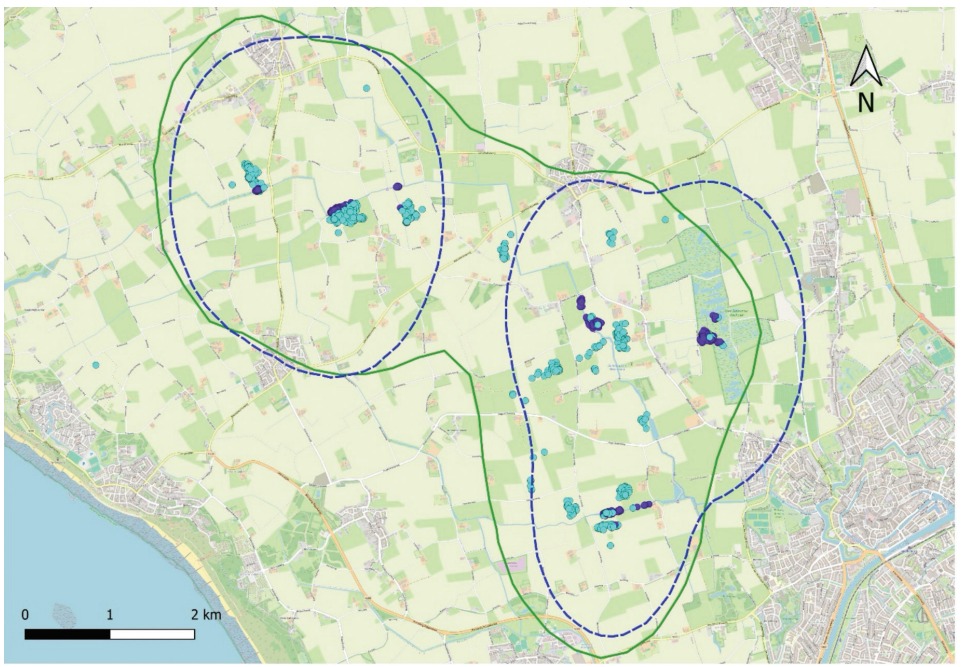


Figure 3. Home ranges of focal bird ZTD in the Netherlands (west of Middelburg) estimated using the 95% Kernel Utilisation Distribution (KUD) method. Light blue points represent daytime GPS fixes and purple points represent nighttime GPS fixes. Green solid polygons indicate the daytime home range, while dark blue dashed polygons indicate the nighttime home range.

greater spatial segregation between daytime and nighttime locations by using different areas at these times (Fig. 2). For AAF, daytime locations were primarily associated with agricultural foraging areas, whereas nighttime locations were concentrated around nearby wetland roosting sites. Core use areas (50% KUD) showed a similar pattern, with AAF having a more concentrated daytime range than ZTD (Table 3).

Spring migration and staging of birds tracked from the Netherlands

Spring 2025 migration from the Netherlands commenced in early March, with marked variation between the two individuals in route, staging behaviour and migration duration. Return migration distances ranged from 2,064–2,533 km and took 9–26 days, with 40.8–87.0% of the total distance flown over sea (Figs. 1C & 1D, Table 2). AAF undertook a rapid return migration, reaching Iceland within nine days, 87% of the total distance being over sea (Fig. 1C, Table 2). The migration included long offshore flights across the North Sea, interspersed with short periods spent resting on the water (n = 5), before landfall in Scotland, a 7-day stop-over in north Scotland and a direct crossing to Iceland. In contrast, ZTD followed a more terrestrial route through England and Scotland via a series of inland

Table 3. Kernel utilisation distribution (95% and 50% KUD) home-range estimates (ha) for two Whooper Swans wintering in the Netherlands.

Period	Daytime (ha)		Nighttime (ha)	
KUD %	95%	50%	95%	50%
ZTD (hourly fixes)	2,768	612	2,402	545
AAF (winter 2024/25, 10–20 min fixes)	1,575	194	1,912	310
AAF (winter 2025/26, hourly fixes)	2,088	183	3,045	599

and coastal staging sites before its final sea crossing from the Outer Hebrides (Fig. 1D). Seven stopovers lasted 0.4–8.8 days (mean ± s.d. = 3.1 ± 3.10).

Despite contrasting strategies, both individuals returned to the Fljótsheiði area in northern Iceland and completed migration by early April.

In spring 2026, AAF again migrated from the Netherlands to Iceland, covering 2,075 km in 13 days. Unlike the previous year, it undertook a direct transoceanic flight without stopping on land. This continuous crossing covered 1,861 km in 3.5 days (84 h), representing 89.7% of the total migration distance remaining entirely offshore throughout (Fig. 1C).

Update on colour-marked birds sighted in the Netherlands

Since the review by Brides *et al.* (2022) on interchange between the Icelandic and NME populations, a further 13 Icelandic-ringed Whooper Swans have been recorded in the Netherlands, bringing the total to 25 (0.3% of the 9,055 Whooper Swans ringed in Iceland between 1934 and 2025). Twenty were recorded within the core areas used by the two GPS-tracked swans, including 18 in Friesland and two in Zeeland. Seven individuals were recorded during winter 2024/25 and eleven during winter 2025/26, corresponding to the winters covered by the present GPS-tracking study, with several birds observed in multiple winters. Overall, the Province of Friesland remains the principal region of occurrence for Icelandic-ringed birds in the Netherlands (Fig. 1E, Table 4).

Discussion

This study provides the first GPS-tracking evidence of Whooper Swans migrating from Iceland to mainland Europe, documenting movements from Iceland to the Netherlands and subsequent return migrations to Iceland. Although based on only two tracked individuals wintering in the Netherlands, these findings are interpreted in the context of the wider GPS-tagged cohort and long-term resightings data from colour-marked swans. One individual repeated this migration in successive years, confirming that such movements represent consistent wintering behaviour rather than isolated events. Colour-ring observations have previously demonstrated that Icelandic



Figure 4. Whooper Swan AAF (before it was tagged) with its partner AAD and two cygnets (36T and 37F) in the Netherlands, January 2024. Photograph by Douwe Struiksma.

birds occasionally winter on mainland Europe (Gardarsson 1991; Newth *et al.* 2007; Brides *et al.* 2022), but the GPS tracking data provide new insight into the routes, staging behaviour and timing of these movements. The extensive oversea crossings and prolonged staging in Britain prior to crossing the North Sea highlight the significance of Britain as a staging region for individuals continuing to mainland Europe. The findings thus demonstrate that overlap of birds from the Icelandic and NME flyways can occur during full annual-cycle migrations, without individuals switching populations and migrating to new breeding areas.

Updated analysis of colour-ring data further supports Iceland–Netherlands connectivity. Most re-encounters occurred in Friesland and Zeeland, matching wintering areas used by the GPS-tracked birds. Ringing origins were from geographically dispersed parts of Iceland, confirming that wintering in mainland Europe is not restricted to a discrete breeding subpopulation, but reflects broader variation in wintering behaviour within the Icelandic population.

Although both birds followed broadly similar autumn migration routes via Britain prior to crossing the North Sea, their spring migrations differed markedly. One undertook relatively rapid, largely oversea migrations, including a direct transoceanic flight from the Netherlands to Iceland in 2026, whereas the other followed a more terrestrial route through England and Scotland before its final sea crossing from the Hebrides. Despite being based on only two individuals, these contrasting routes suggest that Icelandic Whooper Swans may exhibit flexibility in migration behaviour, consistent with patterns documented in other large migratory waterbirds (Kölzsch *et al.* 2016), where route choice may vary in response to environmental conditions and energetic constraints.

Table 4. Individuals ringed in Iceland and resighted in the Friesland and Zeeland regions of the Netherlands. Age classes: A = adult; C = first-calendar year (cygnet).

Ring	Age	Sex	Ringing date	Ringing location	Season(s) in the NLs	Region within the NLs	Comments
23H	A	M	06/08/2023	Kálfborgarárvatn	2024	Zeeland	Partner of Yellow ZTD; observed in Belgium in 2025.
23J	A	F	15/08/2021	Kálfborgarárvatn	2025	Friesland	Previous GPS tagged bird wintered entirely in Britain for 2024/25 winter.
37F	C	F	12/08/2023	Kálfatjarnir	2023	Friesland	Cygnet of AAD & AAF
36T	C	F	12/08/2023	Kálfatjarnir	2023	Friesland	Cygnet of AAD & AAF
44H	A	M	14/08/2023	Miklavatn, Skagafjörður	2024, 2025	Friesland	
45A	A	F	07/08/2024	Sandvatn, Mývatnsheiði	2025	Friesland	Partner of 65T
4XX	A	F	14/08/1995	Anavatn, Jokuldalsheidi	1995	Friesland	
55F	A	M	10/08/2024	Hrappsstaðaselstjörn	2025	Friesland	
54H	C	M	08/08/2025	Kálfatjarnir	2025	Friesland	Cygnet of AAD & AAF
54J	C	F	08/08/2025	Kálfatjarnir	2025	Friesland	Cygnet of AAD & AAF
54U	A	F	08/08/2025	Hrappsstaðaselstjörn	2025	Friesland	
65T	A	M	08/08/2024	Sandvatn, Mývatnsheiði	2024, 2025	Friesland	Partner of 45A
6IA	A	F	18/08/1996	Anavatn, Jokuldalsheidi	1996	Friesland	
FLT	A	F	15/08/2023	Miklavatn, Skagafjörður	2024, 2025	Friesland	
AAD	A	M	07/08/2022	Kálfatjarnir	2023, 2024, 2025	Friesland	Partner of AAF
AAF	A	F	08/07/2022	Kálfatjarnir	2023, 2024, 2025	Friesland	Partner of AAD
ZTB	A	M	17/08/2015	Hrappsstaðaselstjörn	2017, 2018	Friesland	
ZTD (orange)	C	M	17/08/2015	Hrappsstaðaselstjörn	2017, 2018, 2019	Friesland	Cygnet of ZTB
ZTD (yellow)	C	F	10/08/2018	Brunnvatn, Fljotsheidi	2024	Zeeland	Partner of 23H; observed in Belgium during 2025
ZTF	C	M	17/08/2015	Hrappsstaðaselstjörn	2017, 2018, 2019	Friesland	Cygnet of ZTB

Upon arrival in the Netherlands, both tagged birds occupied winter home ranges centred on agricultural feeding areas and nearby wetland roost sites. Similar patterns of winter home range and inter-annual site fidelity have been widely documented in Whooper Swans wintering in Britain and Ireland, where individuals typically return to the same restricted wintering areas across multiple years (Black & Rees 1984; Rees *et al.* 2002). The repeated use of the same wintering area by AAF across two successive winters is consistent with this behaviour, although additional data from more individuals and winters are required to determine whether Icelandic Whooper Swans wintering in mainland Europe exhibit comparable levels of site fidelity.

Our findings have implications for conceptualising Whooper Swan migratory flyways. The Icelandic and NME populations have traditionally been treated as occupying largely discrete flyways, yet the GPS and colour-marking data presented here demonstrate that interchange between them does occur through the complete annual migration cycle. Although the frequency of these movements remains uncertain, the present study shows that flyway boundaries are not absolute. Even relatively infrequent interchange has implications for flyway-based population assessments because it introduces uncertainty into the assignment of individuals to breeding populations and wintering systems (Brides *et al.* 2022). Maintaining a well-connected network of wetlands across the flyway, including key staging areas such as the Ouse Washes (Brides *et al.* 2026), remains critical. Recent analysis of GPS-tracking data has also shown that less than one-third of hourly locations recorded for Icelandic Whooper Swans occur within protected areas, with substantial variation between individuals (Vickers *et al.* 2026), further highlighting the importance of the wider landscape when assessing the conservation requirements of this population. Although modelling suggests that increased foraging effort may partially offset increasing competition at major wintering sites (Wood *et al.* 2019), individual responses to competition are likely to vary. Competition at traditional wintering sites may encourage some individuals to exploit alternative wintering areas, including mainland Europe, although the present study cannot determine the drivers underlying these movements. The Netherlands already supports a wintering population of Whooper Swans from the NME flyway, and the presence of Icelandic birds within these flocks suggests that overlap between the two flyways does occur. Overall winter abundance in the Netherlands has not undergone significant changes in the past decade, although recent figures suggest some tendency to decline (Hornman *et al.* 2025). Similar observations have been made in the Province of Friesland, which is regarded as one of the core areas for Icelandic Whooper Swans, but interestingly numbers in census units where the two tagged individuals were recorded do not fit in this recent decline (Sovon Vogelonderzoek unpubl. data). In the Province of Zeeland, in the southwestern part of the country, and close to UK wintering areas, numbers have significantly increased over the past decade, but it remains speculative if this is mainly driven by Icelandic Whooper Swans.

Icelandic Whooper Swans' migration to wintering areas further from the breeding grounds runs counter to the widespread "short-stopping" trend observed in many migratory waterbird species, whereby individuals increasingly winter closer to breeding areas in response to milder winters and changing environmental conditions (*e.g.* Linssen *et al.* 2023; Nuijten *et al.* 2020; Lehikoinen *et al.* 2013). Given that Whooper Swan migratory behaviour is sensitive to climatic conditions, particularly temperature (Månsson & Hämäläinen 2012; Stirnemann *et al.* 2012), the southward extension of Icelandic-breeding birds' wintering range to mainland Europe suggests that factors other than climate may be involved. The benefits of exploiting abundant agricultural food resources may offset the additional energetic costs of the longer migration, making wintering in mainland Europe energetically viable. This is consistent with competition-based migration theory, whereby some individuals may travel further to exploit less crowded wintering areas despite the additional costs of migration (Hedh *et al.* 2024).

Although Whooper Swan migration from Iceland to mainland Europe appears to involve only small numbers of individuals at present (Brides *et al.* 2022), the combination of GPS tracking and colour-ring observations indicates that repeated wintering in mainland Europe can occur. The frequency of these movements, and the extent of interchange between the Icelandic (breeding) and North Mainland European (breeding) flyway-populations, however remain uncertain. Continued tracking and coordinated international monitoring will be essential for determining how commonly these movements occur and whether their frequency changes over time.

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