Migration routes and conservation status of the Whooper Swan *Cygnus cygnus* in East Asia

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Abstract

The migration routes and migratory patterns of Whooper Swans *Cygnus cygnus* summering in western Mongolia have not previously been described and the status of the East Asian population is currently uncertain. Here we therefore use a combination of satellite tracking data, sightings of colour-marked individuals, published literature and expert knowledge to determine their distribution and site-use more precisely. Results indicated that the swans' summer distribution extended further than had previously been recorded, with three new wintering areas (in Xinjiang, Qinghai-Gansu and Beijing) identified for the species in China. The East Asian Whooper Swan population was estimated to number 57,690 individuals, generating a new 1% threshold of 577 birds for determining sites of international importance for the species in the region. Using count data from winters 2011/12–2018/19, we identified eight wintering sites of international importance for the species in China, six in South Korea and 14 in Japan. Annual variation in national count totals highlighted the need to improve survey effort in China. Individual swans showed considerable within-winter fidelity to their wintering sites, with limited exchange between wintering areas. Migration duration, stopover duration, the number of stopover sites and migration legs were significantly greater in spring than in autumn, whilst migration speed was slower in spring than in autumn. Assessment of the habitats frequented found seasonal variation in the proportion of time that the swans spent on arable crops, pasture, wetlands and open water. From their GPS locations, 46.9%, 25.5%, 35.3% and 0.0% of the tagged swans were in protected areas during the summer, autumn staging, winter and spring staging periods, respectively. Our results provide a basis for the conservation of Whooper Swans in East Asia and illustrate the need for improved monitoring and further research into their migration, particularly for informing the protection and management of the main stopover and wintering sites for the species in China.

Key words: key sites, migration route, population size, satellite tracking.

Whooper Swans *Cygnus cygnus* breed across Eurasia from Iceland to Far East Asia, and migrate to winter across temperate Europe and Central Asia to China and Japan (Brazil 2010). Historically, five populations have been described based on their largely discrete wintering and breeding areas: the Icelandic, Northwest Mainland Europe, Black Sea/East Mediterranean, Caspian/West Siberian and East Asian populations (Rees *et al.* 2019; Wetlands International 2019). The little-known East Asian population was estimated to number *c.* 60,000 individuals at the end of the 20th century (Miyabayashi & Mundkur 1999; Wetlands International 2019) but the population trend remained uncertain (Wetlands International 2019). More recently, counts of 6,221 Whooper Swans wintering in eastern China, 5,737 in South Korea and 29,884 in Japan during winter 2010/11 (Cao *et al.* 2008; Jia *et al.* 2016) suggested a minimum population size of 41,842 birds. The Japanese-wintering population trend has been reported as stable in recent years (Ministry of the Environment 2019; Rees *et al.* 2019), following an increase during the second half of the 20th century (Albertsen & Kanazawa 2002), and their migration routes from Japan have been documented by satellite telemetry (Shimada *et al.* 2014). Little is known about the numbers and trends of Whooper Swans wintering in China, and the breeding origins and migration routes of Chinese-wintering Whooper Swans are poorly understood, although some stopover sites used by Whooper Swans have been identified (Zhang *et al.* 2016; Li *et al.* 2018; Jia *et al.* 2019).

The establishment of effective networks of protected areas for migratory waterbirds is vital for sustaining migratory bird populations throughout their annual cycle. One way to contribute rapidly to this process is to compare the numbers of individuals using monitored wetland sites across recent years, in order to assess their numerical importance relative to the total numbers of individuals in the overall flyway. Another means of identifying important sites (especially in staging areas) is to deploy tracking devices to see where, when and how many birds use a staging site *en route* between breeding and wintering areas. Protection of important stopover/wintering/summering areas is crucial to ensure that migratory species have a sufficient network of suitable, secure sites and habitats available to them throughout the year, taking into consideration the effects of rapid land use and climate change on sites along their flyways. Yet knowledge about the birds' use of sites along migration routes is still lacking for many waterbirds in Far East Asia (Wang *et al.* 2018a).

Although some key sites and flyway population abundance had been identified before 2000 (Miyabayashi & Mundkur 1999), our knowledge about the Whooper Swan in Far East Asia has remained rudimentary and urgently needs updating. The aim of this analysis was to improve existing knowledge of Whooper Swan distribution, migration routes, stopovers, habitat use and the conservation status of main areas used by birds that summer in western Mongolia, and to obtain a better understanding of the Chinese-wintering Whooper Swans in relation to those monitored very well over many years in Japan and South Korea. To do so, we combined results from field surveys with expert knowledge, GPS tracking and ring resightings, to generate updated population estimates, ascertain historical trends, identify key wintering sites, and describe the migration and distribution of the species in China, South Korea and Japan, the main wintering areas for Whooper Swans in Far East Asia. Additionally we compared migration parameters recorded for GPS-tagged swans during their spring and autumn migrations, to provide baseline information on the swans' migration phenology in this flyway.

Methods

Migration and ring re-sighting data

Thirteen adult flightless Whooper Swans were caught on lakes at their summering grounds in Mongolia. During the moulting period, researchers used boats to catch flightless swans on lakes by hand or with hand-nets, or used boats to drive the swans to the shore and into funnels nets and corrals. Swans were weighed, measured, sexed using DNA analysis of pulled feather samples, and fitted with Debut45 GPS/GSM (Global Positioning System/Global System for Mobile Communications; Druid Tech, China) loggers mounted on neck collars (45.5 g, constituting < 1% of total body mass of the birds). These devices record instantaneous time, latitude, longitude, altitude, temperature, humidity, light intensity, air pressure, velocity and voltage at pre-set intervals (Supporting Materials Table S1). The swans were caught, and loggers deployed, in accordance with guidance and permission from the Ministry of Nature, Environment and Tourism (No. 06/2008) of Mongolia. The duty cycle for recording GPS positional fixes varied from one fix per hour to one fix per day, depending on transmitter type and battery condition. Of the 13 tagged birds, nine recorded at least one complete one-way migration (see Table S1 for full details). First-day movement data after birds were captured and tracked, and last-day data before the birds died or their loggers failed, were excluded from the analyses.

Migration data were also collected by searching the Web of Science database for relevant studies, using the expression: (GPS OR Argos OR PTT OR CTT OR (satellite* AND (track* OR transmitter* OR telemetr*))) AND (Whooper Swan*). Locations and corresponding timestamps of individual migration movements, or of representative population migration routes (*i.e.* synthesised migrations), were extracted from published sources (Newman *et al.* 2009; Shimada *et al.* 2014; Supporting Materials Table S2).

Re-sighting data from Whooper Swans marked with neck collars (caught in the same way) in Mongolia in July–August between 2010–2019 (n = 96: 88 adults, 6 juveniles, 2 of unknown age) and from collared Whooper Swan marked in Japan in November–August between 1970–2009 (n = 19, all of unknown sex and age) were also used to identify migration range, wintering site fidelity and exchange between winter populations (Supporting Materials Table S3). The ring resighting data were collated by the Mongolia Bird Band Center, from photos and location uploaded by experienced observers.

Distribution of the East Asian population

An overview of the distribution of the East Asian Whooper Swan population was initially based on the distribution map published by BirdLife International and Handbook of Birds of the World (2019). This was revised in line with counts made of the species in its wintering range (see *Abundance estimates and trends in the main wintering population* section in *Methods*), and by links established between the wintering and summering areas derived from satellite-tracking data, ring resightings and expert knowledge (see *Migration data* section in *Methods*). All these sources of knowledge were combined to produce a revised and updated map of the distributional range and migration routes presented here. GPS points for tracked individuals during the summer were extracted to validate and supplement expert knowledge on the breeding distribution of the species in East Asia. All maps were managed and illustrated in ArcGIS 10.2 (ESRI 2013).

In October 2019, the "*2nd International Symposium on Developing Effective Coordinated Monitoring of East Asian Waterbirds in the 21st Century*" was held in Beijing, China. During the symposium, 17 experts from six countries in the East Asian flyway discussed and contributed further to the delineation of the migration routes and distribution of the Whooper Swan in East Asia (Supporting Materials Table S4). The experts also advised on literature sources and unpublished data, used to support modification of the distribution maps.

Abundance estimates and trends in population size

As the East Asian Whooper Swan population winters mainly in China, South Korea and Japan (BirdLife International and Handbook of Birds of the World 2019), it has been convenient historically to divide this population into three wintering subpopulations for monitoring the overall numbers in East Asia, a process we continue here.

For the China subpopulation, estimates from winters 1987/88–2010/11 were obtained from archive data used to support the analysis reported by Jia *et al.* (2016). A survey of Whooper Swans that covered the known historical and current distribution in January 2019 was used to assess abundance in China by summing all the counts at each of the wintering sites in each province.

In Japan, annual mid-winter (mid-January) surveys of waterfowl have been conducted since 1970 by the Ministry of the Environment with the assistance of prefectural governments. This nationwide survey covers all of the principal sites for swan, goose and duck species throughout the country during the non-breeding season (Ministry of the Environment 2019).

The Korean Ministry of Environment and its associated institutes, the National Institute of Environmental Research (until 2007) and the National Institute of Biological Resources (since 2008), have also conducted an annual nationwide census at most lakes, reservoirs, seashore and bays known to be important for waterbirds during the non-breeding period. The coordinated two-day field counts are made annually in mid- or late January by ornithologists, avian researchers and experienced birdwatchers, in order to estimate the distribution and abundance of waterbirds wintering in South Korea.

Simple linear regressions were applied to detect trends in abundance in each country, with log-transformed abundance estimates as the dependent variable, and year as the independent variable. Trends in count data for long-lived waterbird species may be temporally autocorrelated (*e.g.* Wood *et al.* 2019), so we initially tested for autocorrelation in the linear regression residuals, using the nlme package in Program R (Pinheiro *et al.* 2020; R Core Team 2020). Inspections of the resulting autocorrelation plots found statistically significant ($P < 0.05$) residual temporal autocorrelation in the regression models for the Japanese count data, but not for China and South Korea. In order to evaluate the country-specific linear trends in counts, generalized least squares autoregressive models therefore were fitted to allow for model errors to be correlated (Pinheiro *et al.* 2020). According to the year in which significant residual autocorrelation was detected, each model contained the following autocorrelation structure: China = 0, South Korea = 0, and Japan = 6. Efron's R^2 was used to quantify the goodness of fit of each model (Efron 1978); as this pseudo R^2 represents the explained variance and strength of correlation between actual and predicted values, it is thus analogous to the true R^2 (which cannot be estimated for generalized least squares regression models with autocorrelation structures). For each model Efron's R^2 was calculated as:

$$R^2_{Efron} = 1 - (\Sigma(y - \hat{y})^2)/(\Sigma(y - \bar{y})^2),$$

where y represented the dependent variable (transformed annual counts), $\hat{y}$ was the model's predicted value, and $\bar{y}$ was the mean value of y across all years (Efron 1978).

Important wintering sites for Whooper Swans in China and South Korea were determined from count data recorded by the authors or from the literature, for the period 2011/12–2018/19, with sites where Whooper Swan numbers exceeded 1% of the flyway population estimate considered of international importance for the species in East Asia (following Ramsar Convention criteria; Ramsar Convention 2017). Sites and counts were aggregated if the distance between them was < 30 km, which is considered to be the maximum commuting distance for Whooper Swans moving within a site (Henty 1977).

In Japan, the swans mainly used coastal areas. Because the swans fly from their wetland roosts to forage on farmland and other habitats during the day, where they are counted, it was impossible to identify single waterbodies as key sites, as was the case in China. Instead, their abundance each year was estimated for a 5 × 5 km resolution grid, covering all Whooper Swan wintering areas in Japan. Grid squares holding > 125 swans were extracted and the number of Whooper Swans counted in those cells were assigned to the nearest roost sites (most known roosts were areas of open water that provided safe overnight resting places), based on expert opinion. Any of these roost sites which held ≥ 1% of the East Asian population size estimate at least once during the study were considered to be key sites for the species in Japan.

Migration parameters

Wintering/summering/stopover sites were identified using the method of Wang *et al.* (2018b), which in brief was based on a threshold of daily movement (150 km d^{-1}) and single movement segment (300 km) used to separate sites and determine migration. A site where individuals remained within a predefined area for > 2 days during migration was defined as stopover site (Kölzsch *et al.* 2016), and the number of stopovers was calculated accordingly. Migration duration was calculated as the time the bird took to travel (including stopovers) between the last position derived at the summering site and first at the wintering site (autumn migration) or between the last position on the winter quarters and the first at the summering site (spring migration). Stopover duration was the sum of days spent at all stopover sites during each migration season. Thus, days spent travelling (total travel days) was calculated as the total migration duration minus the stopover duration. A "migration leg" was defined as the journey that connected successive wintering, stopover or summering sites, summed to provide the number of migration legs involved in each migration episode (spring or autumn). Migration distance was defined as the cumulative orthodrome distance of adjacent locations between wintering and summering sites, excluding movement within stopover/wintering/summering sites, and step length was calculated as the migration distance divided by the number of migration legs during each migration. Displacement was calculated as the orthodrome distance between the point at which its migration began and the point at which it ended, being the shortest distance between these points. The straightness index was calculated for each swan as the ratio between the perfectly orientated orthodrome distance between the last location of a swan before departure to the first location after arrival, divided by the total migration distance actually taken along the path followed by that individual bird (Benhamou 2004). Migration speed was calculated as the migration distance divided by migration duration, and the travel speed was calculated by dividing migration distance by the total number of travel days. Sex differences in migration patterns were not included in the analysis because most adult Whooper Swans are paired (Einarsson & Rees 2002; Shchadilov *et al.* 2002), so the birds were likely to have been travelling with their long-established mates.

Comparison of migration parameters in spring and autumn

Linear mixed models were used to examine the effect of season (spring or autumn) on migration parameters, including migration duration, migration speed, migration distance, straightness index, travel days, travel speed, number of stopovers, stopover duration and step length. Each migration parameter was treated separately as the response variable, "Season" as the fixed effect and "Logger" (effectively the identity of the bird) as a random effect. Models were fitted using lme4 package (Douglas *et al.* 2012) in Program R (R Development Core Team 2020). All estimates presented in the tables and text are based on these estimated means (± s.d.) unless otherwise stated.

Land use type and conservation status at stopover sites

Land cover types across China during 2017 were mapped at a 10 m × 10 m resolution, based on 10 main habitat categories (cropland, forest, grassland, shrubland, wetland, water, tundra, permanent snow/ice, bare land, artificial surfaces) by the Ministry of Education Key Laboratory for Earth System Modeling, Department of Earth System Science, Tsinghua University, Beijing (Gong *et al.* 2019). Seasonal wetlands might be misidentified as bare land due to the mismatch between the dates of land cover sampling and the use of these areas by the birds. For this reason, sites visited by tracked swans that fell within bare land pixels we retrospectively reclassified, based on Google Earth or Landsat images taken at the approximate date of use by each bird. We also retrospectively reclassified forest and artificial surfaces pixels that Google Earth and Landsat images confirmed were misclassified in the original land cover type classification. These reclassified land use types were re-entered into the database for use in this study. In order to estimate the land use types exploited by tracked swans and the extent to which they occurred within protected areas, tracking locations were restricted to those positions associated with flight speed (the distance between two points divided by the time between two points) < 2 m s^{-1} (Wang *et al.* 2018a). The resulting subset of positions were then overlapped upon the land cover dataset and protected areas, and analysed in ArcGIS 10.2 (ESRI 2013). Boundaries for protected areas in Mongolia were extracted from the world database on protected areas (UNEP-WCMC 2017), and the boundaries of 471 national nature reserves in China were obtained from the Resource and Environment Data Cloud Platform (http://www.resdc.cn/).

Results

Distribution range of the East Asian population

Accumulated expert opinion and the results of the telemetry studies indicate that the summer range of the East Asian Whooper Swan population extends from the Yenisei River (69°35'N, 84°22'E) in the west across to the Anadyr River in the east (64°37'N, 178°44'E). This is more extensive than previously recorded, in that it now includes the northwest part of the Xinjiang Uygur Autonomous Region, Beijing City and the border area between China and Mongolia east to the Amur River region in Russia (Fig. 1). Following inspection of the satellite tracks, ring resightings and winter survey data, the wintering distribution has also been extended to include Xinjiang, Qinghai and Gansu Provinces, and Beijing City in China, but now excludes the Yangtze River Basin, where recent intensive surveys have found consistently few wintering individuals (Fig. 1).

Migration tracks were recorded and reviewed for 70 East Asian Whooper Swans (47 autumn and 65 spring migrations), including 13 birds caught in Western Mongolia (this study), 10 birds caught in Eastern Mongolia (five autumn and two spring tracks from Newman *et al.* 2009) and 47 birds caught in Japan (33 autumn and 57 spring tracks from Shimada *et al.* 2014). Nine of the 13 birds caught in Western Mongolia in this study returned complete data (Fig. 2). They migrated through the Gobi Desert between Mongolia and northern China, and wintered in Gansu Province (n = 1), Qinghai Province (n = 1), the border of Henan Province, Shaanxi Province and Shanxi Province (n = 6) and in Shandong Province (n = 1). Of the 10 birds caught in Eastern Mongolia, five provided full data as they migrated through northeast China, across the Bohai Sea to South Korea (n = 4) and to Shandong Province, China (n = 1, Fig. 2). The birds caught in Japan in general migrated along Amur River and Kolyma River, to summer in eastern Russia.

Ninety-six birds marked with neck collars in western (n = 64) and central (n = 32) Mongolia were reported in China (251 sightings of 96 individuals) and South Korea (five sightings of one individual).

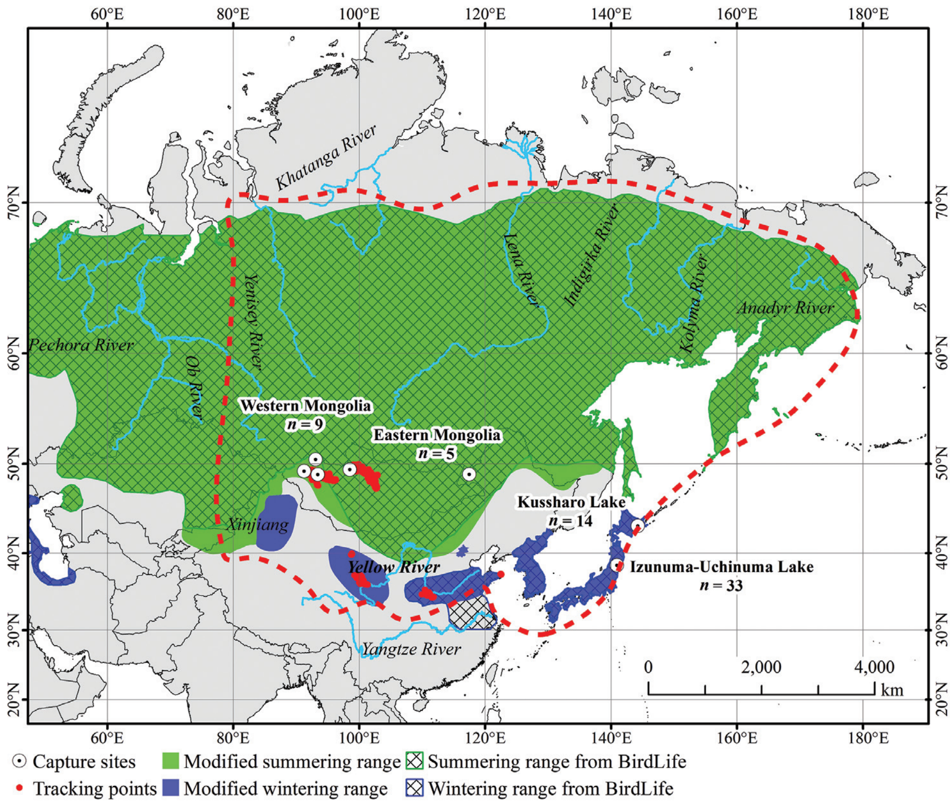

Figure 1. Revised distribution map for the Whooper Swan in East Asia, including summering (green: middle–eastern Siberia in Russia, south to north Mongolia, and northwest China), wintering ranges (blue: mainly in central and eastern China, South Korea and Japan) and flyway range (red dashed line, birds summered in Mongolia and Russia, wintered in China, South Korea and Japan), modified from BirdLife International and Handbook of Birds of the World (2019). Revisions to the summer range were based on tracking data (red points, which represent GPS locations recorded for each individual between their arrival and departure at the summering grounds from 1 May–30 October) and expert knowledge. The revised winter range was based on field survey data and expert knowledge (see *Methods* for details). Sixty-one migrations were recorded for birds caught and tagged in two areas during summer (in Western and Eastern Mongolia) and in two wintering areas (Kussharo Lake and Izunuma-Uchinuma Lake, Japan) in East Asia. Circles with black dots = capture sites, *n* = number of birds that completed at least one spring or autumn migration (see Supporting Materials Tables S1 & S2 for full details). All the site/area names mentioned in the paper are shown on the map.

Sightings of swans with neck collars in China all fell within the revised winter distribution (Fig. 2). Collared birds largely used wintering areas that were also exploited by tracked birds (*e.g.* in Gansu and Qinghai, *n* = 15; and the middle and lower reaches of Yellow River, *n* = 67), but also used areas (*e.g.* the Xinjiang wintering area, *n* = 12) that

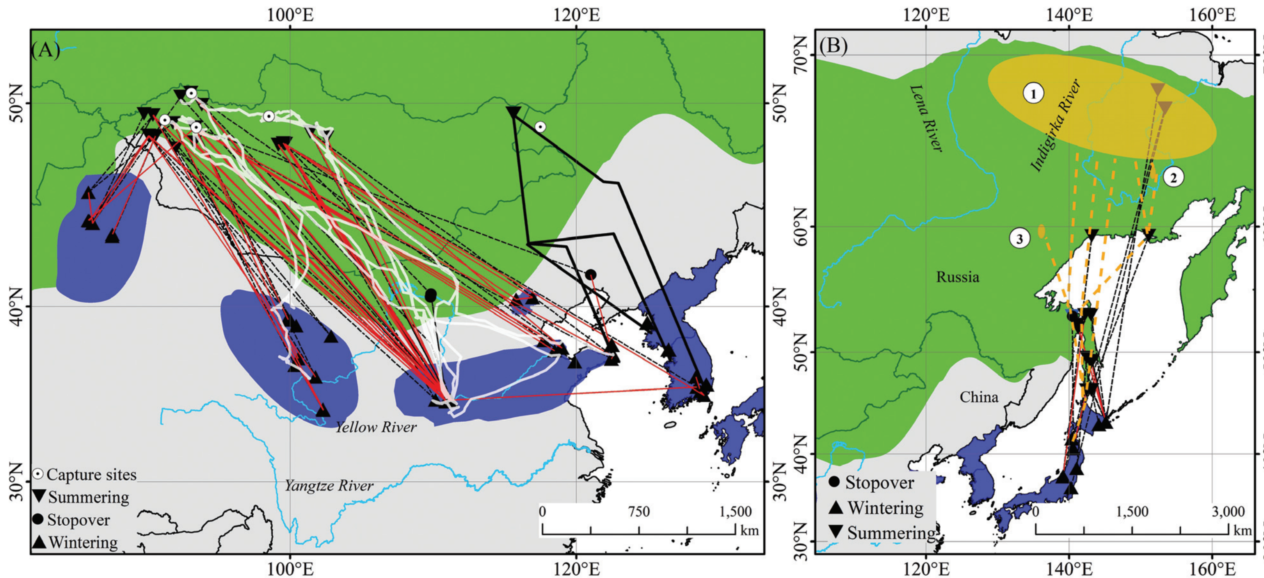

Figure 2. East Asian Whooper Swan flyway, showing migrations recorded for: (A) birds which summered in Mongolia and wintered in China or South Korea, and (B) birds which summered in Far East Russia and wintered in Japan. White solid lines (n = 9) are individuals from the Chinese-wintering population; black solid lines (n = 5) are individuals from the South Korean-wintering population, all of which summered in Mongolia. Orange dotted lines denote representative (synthesised) migration routes, orange shaded areas (with numbers) denote the representative summering/stopover/wintering areas for 47 tracked birds that summered in Russia and wintered in Japan (from Shimada *et al.* 2014), and numbers denote: ① Indigirka and Kolyma Rivers, ② lower Kolyma River, and ③ Marekan Cape vicinity (northern coastal areas of the Sea of Okhotsk). Green and blue shaded areas = revised assessments of the summer and winter ranges, respectively. Inverted and regular triangles = summer and wintering areas used by tracked individual(s), respectively; black solid circles = stopover sites. Red direct solid lines link individual resightings within breeding and wintering seasons in the same year; black direct dotted lines link resightings of individuals that lack resighting from intervening seasons (*e.g.* were seen in their first breeding season and second winter season). Neck-collared birds marked in Mongolia mostly used wintering areas in Xinjiang (n = 12; 12%); Gansu and Qinghai (n = 15; 16%); the middle reached of the Yellow River (n = 51; 51%), Beijing (n = 2; 2%) and the lower reaches of the Yellow River (n = 18; 19%).

had not been visited by tracked individuals (Fig. 2). Sightings of 19 birds marked in Japan used summering/stopover areas in September–June that were exploited by tracked birds (eastern Russia summering area, *n* = 19) (Fig. 2).

Thirty-five of the 96 neck-collared birds from Mongolia that wintered in China and South Korea showed winter site fidelity during 2010/11–2018/19. Twenty-six out of 35 birds sighted in two years were seen at the same wintering sites, seven were seen in three years, one in four years, and one in five years.

Movement between wintering areas was occasionally observed. One bird marked in Mongolia in 2011 was seen in South Korea in January 2012 and 2013, and then reported in South Korea and China in November 2015. It was last sighted on the Yellow River estuary in China in January 2019 (Fig. 2).

Abundance estimates and overall trends

In China, 24,405 wintering Whooper Swans were counted in seven provinces in January 2019, including 5,759 and 5,235 Whooper Swans in Henan and Shanxi Provinces, respectively, 3,723 wintering in Xinjiang, 299 in Qinghai Province, 717 in Gansu Province, 10 in Beijing and 8,660 swans in Shandong Province (Table 1).

Whooper Swan numbers recorded for the three wintering subpopulations from January 1970–2019 showed differing trends. Those wintering in South Korea increased significantly from 1,955 in 1999 to 7,229 in 2018 (Table 2; Fig. 3). The Japanese subpopulation similarly increased between 1970 and the early 2000s, but numbers have stabilised or even declined slightly in recent years. Nevertheless, the overall growth from 11,095 in 1970 to 24,795 in 2019 (Fig. 3) was statistically significant for the whole time-series (Table 2). The trend in China was not significant (Table 2) because of sparse data, despite the fact that the Chinese population estimate increased from 8,915 in winter 1992/93 to 24,405 in 2018/19 (Fig. 3). For January 2015–2019, the five-year average count of Whooper Swans wintering in Japan was 27,307, and for January 2014–2018 the average count of South Korean-wintering swans was 5,978 birds. By adding the number of Chinese-wintering swans in 2019 (24,405 individuals) to these figures, the the East Asian Whooper Swan population was estimated at 57,690, and hence the 1% criterion for this population was 577 individuals.

Based on the new 1% criterion, there were eight wintering sites in China, six in South Korea and 14 in Japan considered to be of international importance for the species, according to the counts recorded in winters 2011/12–2018/19 (Fig. 4, Table 3).

Autumn migration

Complete autumn migrations were obtained for nine Whooper Swans tagged in Western Mongolia in 2017 (Fig. 5, Table 4). These used four different wintering areas: Longyangxia Reservoir in Qinghai Province (*n* = 1), the middle reaches of the Yellow River in Shanxi, Shaanxi and Henan Provinces (*n* = 6), the Rongcheng coast in Shandong Province (*n* = 1) and the Jiuquan wetlands in Gansu Province (*n* = 1).

Mean autumn departure date from summering areas was 22 October (range = 3 October–12 November, see Table 4 for data from individuals), mean arrival date to the

Table 1. Number of Whooper Swans counted in China in winter 2018/19.

Province	Wetland	Count	Month/year
Henan	Yellow River Wetland National Reserve	962	Jan. 2019
	Sanmenxia National Wetland Park	4,797	Jan. 2019
Shanxi	Yellow River Wetland Swan Nature Reserve, Pinglu county	3,250	Jan. 2019
	Shengtianhu Park , Pinglu county	1,200	Jan. 2019
	Yellow River Beach, Pinglu county	783	Jan. 2019
	Duck pond	2	Jan. 2019
	Hancheng Yellow River Wetland Reserve	2	Jan. 2019
Gansu	Linze	18	Jan. 2019
	Akesai	2	Jan. 2019
	Akesai	11	Jan. 2019
	Subei	8	Jan. 2019
	Yumen	6	Jan. 2019
	Yongchang	158	Jan. 2019
	Gaotai	182	Jan. 2019
	Minqin	105	Jan. 2019
	Gahai Lake	79	Jan. 2019
	Gaotai	148	Jan. 2019
Beijing	Huairou Reservoir	10	Dec. 2018
Qinghai	Jura Wetland	4	Dec. 2018
	Ganzi River	2	Dec. 2018
	Naren Wetland	6	Dec. 2018
	Bird Island	1	Dec. 2018
	Tiebujia Estuary	162	Dec. 2018
	Quanwan	124	Dec. 2018
Shandong	Dawenliu management station	1,076	Jan. 2019
	Yiqianer management station	84	Jan. 2019
	Rongcheng coast	7,500	Jan. 2019
Xinjiang	Ili	150	Jan. 2019
	Bo Zhou	268	Jan. 2019
	Shihezi	420	Jan. 2019
	Manas	315	Jan. 2019
	Urumqi	200	Jan. 2019
	Bazhou (Korla)	520	Jan. 2019
	Bachu	750	Jan. 2019
	Tarim River Basin	1,100	Jan. 2019

Table 2. A summary of the results from the regression models of the linear trends in counts for each country. ACS = autocorrelation structure (no. of years) included in the model.

Country	ACS	Parameter	Estimate	s.e.	*t* value	*P* value	Efron's R^2
China	0	Intercept	–14.256	29.104	–0.490	0.650	–
		Year	0.009	0.014	0.625	0.566	0.089
South Korea	0	Intercept	–27.408	6.224	–4.404	< 0.001	–
		Year	0.015	0.003	4.993	< 0.001	0.581
Japan	6	Intercept	–15.944	4.042	–3.944	< 0.001	–
		Year	0.010	0.002	5.014	< 0.001	0.695

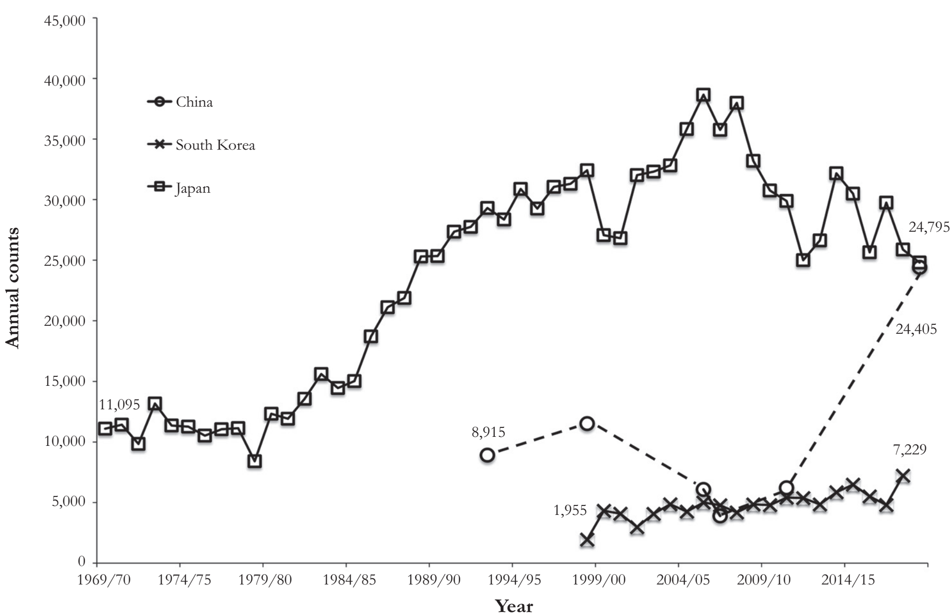

Figure 3. Trends in abundance for the three Whooper Swan subpopulations (wintering in China, South Korea and Japan) in East Asia, based on available counts from January 1970–2019. Estimates for China from 1988–1993 (aggregated maximum counts for each wetland) to 2011 were obtained from Jia *et al.* (2016); those during 2012–2019 were derived from winter surveys (See *Abundance estimates and trends in the main wintering population* in *Results*). Abundance estimates for Whooper Swans in Japan and South Korea were obtained from the annual winter surveys undertaken in January 1970–2019 and January 1993–2018, respectively. Dashed lines connect counts where count data were missing in the intervening years.

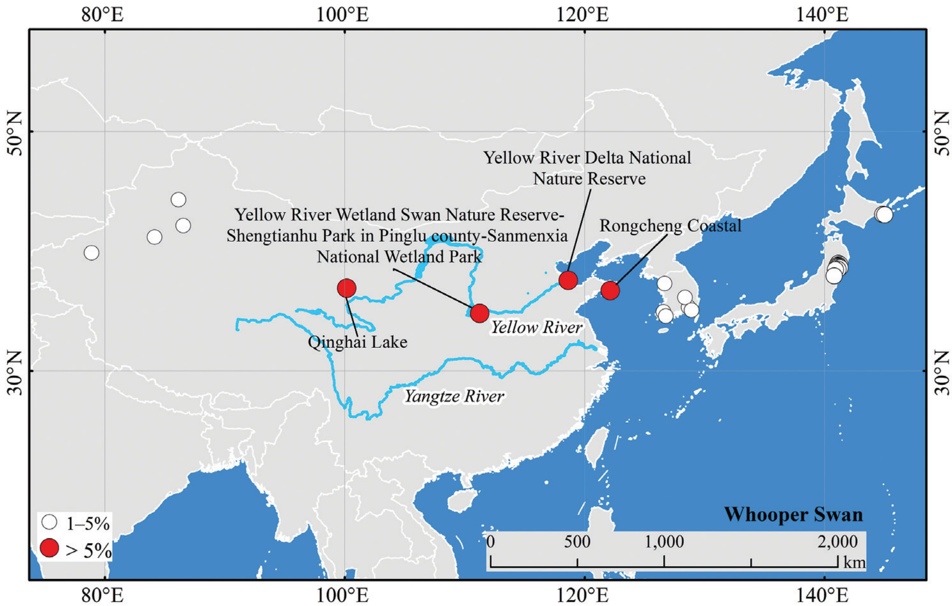

Figure 4. Distribution map of the 21 wintering sites identified as important for Whooper Swans in the East Asian flyway. These include 8 sites in China (four recorded with ≥ 5% and four with ≥ 1% of the flyway population in at least one winter), 6 in South Korea (all with ≥ 1% of the population) and 14 in Japan (all with ≥ 1% of the population). The 1% threshold (577 birds) for identifying internationally important sites was based on the total population estimate for Whooper Swans in East Asia (57,700 individuals), derived by summing the mean of the numbers counted in South Korea in January 2014–2018, in Japan in January 2015–2019, and in China in 2019.

winter quarters was 5 November (range = 7 October–13 November) and mean migration duration was 14.1 days (range = 1.7–29.5 days). The tagged swans used an average of 1.2 stopover sites (range = 0–2) for between 3.2 and 25.0 days. Two birds completed migration non-stop between summering and wintering areas in one leg. Mean migration distance was 2,304 km (range = 1,524–3,094 km), while mean migration speed was 353 km d^{-1} (range = 63–1,449 km d^{-1}). The mean number of travel days was 3.9 (range = 1.7–5.8 days) in an average of 2.2 migration legs (range = 1–3 legs) of mean length 1,220 km (range = 508–2,475 km). Mean straightness index was 0.80 (range = 0.52–0.91) and mean displacement was 1,839 km (range = 993–2,354 km).

Spring migration

Among the nine birds tagged in Western Mongolia that completed autumn migration, six were also tracked for the whole of their subsequent spring migrations (Fig. 5, Table 4). Signals from two individuals (ws003, ws007) were lost in Ordos City, Inner Mongolia Autonomous Region, during spring migration. The spring migration of

Table 3. Maximum counts at key wintering sites of Whooper Swans in East Asia from 2012 to 2019.

Country	Province	Key site	Count	Date
China	Xinjiang	Shihezi-Manas	735	Jan. 2019
	Xinjiang	Hejing-Korla (Bazhou)	> 600	Jan. 2019
	Xinjiang	Bachu-Tumushuke	750	Jan. 2019
	Xinjiang	Tarim River	1,100	Jan. 2019
	Qinghai	Qinghai Lake	2,134	Dec. 2016
	Shandong	Rongcheng Whooper Swan National Nature Reserve	7,500	Jan. 2019
	Shandong	Yellow River Delta National Nature Reserve	1,160	Jan. 2019
	Henan and Shanxi	Yellow River Wetland Swan Nature Reserve-Shengtianhu Park in Pinglu county-Sanmenxia National Wetland Park	10,209	Jan. 2019
South Korea	Gyeonggi-do	Shihwa Lake	579	Jan. 2017
	Jeollanam-do	Useupje Reservoir	652	Jan. 2016
	Jeollanam-do	Gangjin Bay	586	Jan. 2012
	Gyeongsangnam-do	Junam Reservoir	1,831	Jan. 2018
	Gyeongsangbuk-do	Gumi Haepyeong, Nakdong River	599	Jan. 2018
	Busan	Nakdong River Estuary	1,707	Jan. 2014
Japan	Hokkaido	Lake Akkeshi	1,420	Jan. 2016
	Hokkaido	Lake Hichirippunuma	762	Jan. 2019
	Iwate	Kitakami River middle basin	869	Jan. 2016
	Iwate	Kitakami River lower-middle basin	583	Jan. 2019
	Iwate	Kabasawa-tsutsumi Embankment	676	Jan. 2018
	Miyagi	Hasama River upper basin	674	Jan. 2016
	Miyagi	Kaishouren Tsutsumi Embankment	1,155	Jan. 2018
	Miyagi	Lake Izunuma	1,457	Jan. 2016
	Miyagi	Lake Uchinuma	623	Jan. 2017
	Miyagi	Lake Kabukurinuma	865	Jan. 2018
	Miyagi	Kitakami River lower basin	1,913	Jan. 2016
	Miyagi	Naruse River	2,622	Jan. 2019
	Miyagi	Sugusawa Reservoir	1,051	Jan. 2019
	Fukushima	Abukuma River	610	Jan. 2019

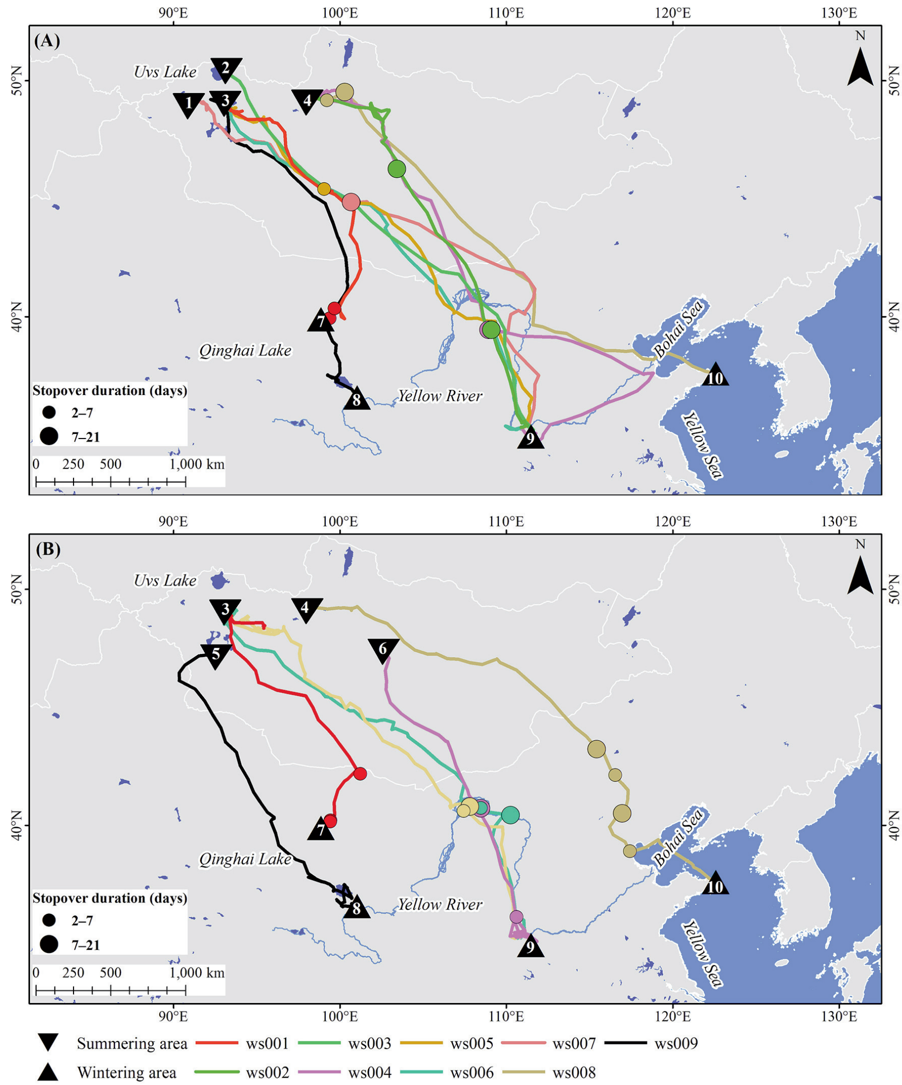

Figure 5. Individual Whooper Swan migration routes taken in: (A) autumn 2017, and (B) spring 2018, by individuals caught in Western Mongolia in summer 2017 (*n* = 9). These birds migrated between their Mongolian breeding grounds and four major wintering sites in China: Jiuquan wetlands (*n* = 1), Longyangxia Reservoir (*n* = 1), the middle reaches of the Yellow River (*n* = 6), and the Rongcheng coast (*n* = 1). Summering areas include: ① Shaazgai Lake, Khovd soum, Mongolia; ② Uvs Lake, Mongolia; ③ Airag Lake, Mongolia; ④ Tunamal Lake, Mongolia; ⑤ Tsagaan Lake, Mongolia; and ⑥ Ogii Lake, Mongolia. Wintering areas include: ⑦ Jiuquan wetlands, Gansu Province, China; ⑧ Longyangxia Reservoir, Qinghai Province, China; ⑨ the middle reaches of the Yellow River, China; and ⑩ the Rongcheng coast, Shandong Province, China.

Table 4. Migration parameters of autumn and spring migrations of Whooper Swans, based on nine complete autumn migrations and six complete spring migrations of nine tracked Whooper Swans.

Logger	Departure date	Arrival date	Migration distance (km)	Migration duration (days)	Migration speed (km d^{-1})	Travel time (days)	Travel speed (km d^{-1})	No. migration legs	Step length (km)	No. stop-over sites	Stop-over duration (days)	Displacement (km)	Straightness index
Autumn													
ws006	05 Nov 2017	12 Nov 2017	2,417	7.13	339	3.92	617	2	1,209	1	3.21	2,138	0.88
ws009	04 Oct 2017	07 Oct 2017	1,545	2.67	579	2.67	579	1	1,545	0	0.00	1,271	0.82
ws003	12 Nov 2017	13 Nov 2017	2,475	1.71	1,449	1.71	1,449	1	2,475	0	0.00	2,241	0.91
ws007	27 Oct 2017	12 Nov 2017	2,842	16.33	174	4.62	615	2	1,421	1	11.71	2,229	0.78
ws001	28 Oct 2017	09 Nov 2017	1,524	12.42	123	5.79	263	3	508	2	6.62	993	0.65
ws005	30 Oct 2017	12 Nov 2017	2,283	13.38	171	4.25	537	3	761	2	9.12	2,015	0.88
ws002	08 Oct 2017	06 Nov 2017	1,865	29.50	63	4.50	414	3	622	2	25.00	1,709	0.92
ws004	26 Oct 2017	13 Nov 2017	3,094	17.46	177	5.58	554	2	1,547	1	11.88	1,598	0.52
ws008	03 Oct 2017	29 Oct 2017	2,691	26.25	102	2.46	1,094	3	897	2	23.79	2,354	0.88
Mean	**22 Oct 2017**	**05 Nov 2017**	**2,304**	**14.09**	**353**	**3.94**	**680**	**2.22**	**1,220**	**1.22**	**10.15**	**1,839**	**0.80**
s.e.	**–**	**–**	**186**	**3.20**	**147**	**0.47**	**121**	**0.28**	**204**	**0.28**	**3.07**	**159**	**0.05**
Spring													
ws006	01 Mar 2018	22 Mar 2018	2,627	20.46	128	5.46	481	3	876	2	15.00	2,131	0.81
ws009	08 Apr 2018	15 Apr 2018	1,818	7.00	260	7.00	260	1	1,818	0	0.00	1,281	0.70
ws001	17 Mar 2018	30 Mar 2018	1,425	13.08	109	2.58	551	4	356	3	10.50	1,087	0.76
ws005	02 Mar 2018	27 Mar 2018	2,472	24.96	99	7.25	341	3	824	2	17.71	1,976	0.80
ws004	01 Mar 2018	23 Mar 2018	1,936	21.25	91	3.12	619	3	645	2	18.13	1,597	0.82
ws008	06 Mar 2018	17 Apr 2018	2,830	41.71	68	10.92	259	5	566	4	30.79	2,354	0.83
Mean	**19 Mar 2018**	**02 Apr 2018**	**2,185**	**21.41**	**126**	**6.06**	**419**	**3.17**	**847**	**2.17**	**15.35**	**1,737**	**0.79**
s.e.	**–**	**–**	**221**	**4.84**	**28**	**1.25**	**63**	**0.54**	**209**	**0.54**	**4.13**	**204**	**0.02**

another individual (ws002) contained a two-week gap covering the early period of the spring migration, which rendered it impossible to document its migration timing, so these birds therefore were excluded from the spring migration analyses.

Mean spring departure date was 19 March (range = 1 March–8 April, see Table 4 for details of individuals), mean arrival date was 2 April (range = 22 March–17 April) and mean migration duration was 21.41 days (range = 7.00–41.71 days). The tagged swans used an average of 2.2 stopover sites (range = 0–4) for between 10.5 and 30.8 days. One bird completed the spring migration non-stop. Mean migration distance was 2,185 km (range = 1,425–2,830 km), while migration speed varied between 68 and 260 km d^{-1} (mean = 126 km d^{-1}). The mean number of travel days was 6.06 days (range = 2.6–10.9 days) in an average of 3.2 legs (range = 1–5 legs) of mean length 847 km (range = 356–1,818 km). The mean straightness index was 0.79 (range = 0.70–0.83) and mean displacement was 1,737 km (range = 1,087–2,354 km).

Comparison of migration parameters in spring and autumn migrations

The linear mixed model revealed significant effects of season, *i.e.* significant differences between spring and autumn migration, for five parameters (Table 5). Migration duration (t = 3.30, β = 8.05, d.f. = 5.20, $P < 0.05$) and stopover duration (t = 3.76, β = 6.16, d.f. = 5.10, $P < 0.05$) were significantly greater in spring than the autumn, while the number of stopovers (t = 2.90, β = 0.86, d.f. = 5.70, $P < 0.05$) and migration legs (t = 2.90, β = 0.86, d.f. = 5.70, $P < 0.05$) were significantly greater during autumn migration. Migration speed (t = –2.61, β = –126.94, d.f. = 4.88, $P < 0.05$) in spring was significantly slower than that in autumn.

Land use type and conservation status at stopover sites

In summer 2017 and 2018, tagged swans (9 individuals, mean ± s.d. = 3,903 ± 2,164 fixes per site) mainly used water (62.2%) and grassland (27.3%), followed by wetland (8.7%, Fig. 6). During the summer period in 2017 and 2018, 46.9% of the tracking fixes were in protected areas (Fig 7, Table 6), including the Har Us Nuur National Park; Khan Khukhii-Khyragas Lake; Orkhon valley; Ulaagchinii Khar Lake; and the Uvs Lake basin in Mongolia.

In autumn 2017 (7 individuals, 11 stopover sites, mean ± s.d. = 264 ± 181 fixes per site), water was most commonly used (82.2%), followed by grassland (8.8%, Fig. 6); and 25.5% of the tracking fixes were within protected areas (Fig 7, Table 6), notably the Valley of Lakes (Boon Tsagaan Lake, Taatsiin Tsagaan Lake, Adgiin Tsagaan Lake and Orog Lake) in Mongolia.

During the 2017/18 winter, tagged swans (9 individuals, mean ± s.d. = 2,692 ± 474 fixes per site) mainly used water (74.1%) and cropland (12.0%), followed by wetland (8.8%) and grassland (3.9%, Fig. 6); and 35.3% of the tracking fixes were within protected areas, including Qinghai Lake in Qinghai Province, Yellow River Wetlands in Henan Province and Rongcheng Whooper Swan National Nature Reserve in Shandong Province.

In spring 2018 (5 individuals, 13 stopover sites, mean ± s.d. = 422 ± 172 fixes per site),

Table 5. Statistical parameters of linear mixed models to predict 11 migration parameters in autumn 2017 and spring 2018, based on nine complete autumn migrations and six complete spring migrations of nine tracked Whooper Swans. Migration duration and stopover duration were significantly greater in spring than the autumn, while the number of stopovers and migration legs were significantly greater than the autumn migration. Migration speed in spring was significantly slower than that in autumn.

Variable	Value	s.e.	*t* value	*P* value
Migration distance (km)				
Intercept	2,303.88	181.41	12.70	< 0.001
Factor (season) spring	–95.80	207.93	–0.46	0.660
Migration duration (days)				
Intercept	14.09	3.56	3.96	0.003
Factor (season) spring	8.05	2.44	3.30	0.020
Migration speed (km d^{-1})				
Intercept	353.09	141.63	2.49	0.037
Factor (season) spring	–126.94	48.65	–2.61	0.049
Travel days (days)				
Intercept	3.94	0.73	5.39	< 0.001
Factor (season) spring	2.11	1.16	1.82	0.091
Travel speed (km d^{-1})				
Intercept	680.30	100.40	6.77	< 0.001
Factor (season) spring	–261.60	158.80	–1.65	0.123
Number of migration legs				
Intercept	2.22	0.34	6.46	< 0.001
Factor (season) spring	0.86	0.30	2.90	0.029
Step length (km)				
Intercept	1,220.39	204.30	5.97	< 0.001
Factor (season) spring	–263.23	166.81	–1.58	0.178
Number of stopover sites				
Intercept	1.22	0.34	3.55	0.006
Factor (season) spring	0.86	0.30	2.90	0.029
Stopover duration (days)				
Intercept	10.15	3.24	3.13	0.013
Factor (season) spring	6.16	1.64	3.76	0.013
Displacement (km)				
Intercept	1,838.68	155.07	11.86	< 0.001
Factor (season) spring	9.10	18.34	0.50	0.641
Straightness index				
Intercept	0.80	0.04	21.84	< 0.001
Factor (season) spring	–0.02	0.06	–0.26	0.800

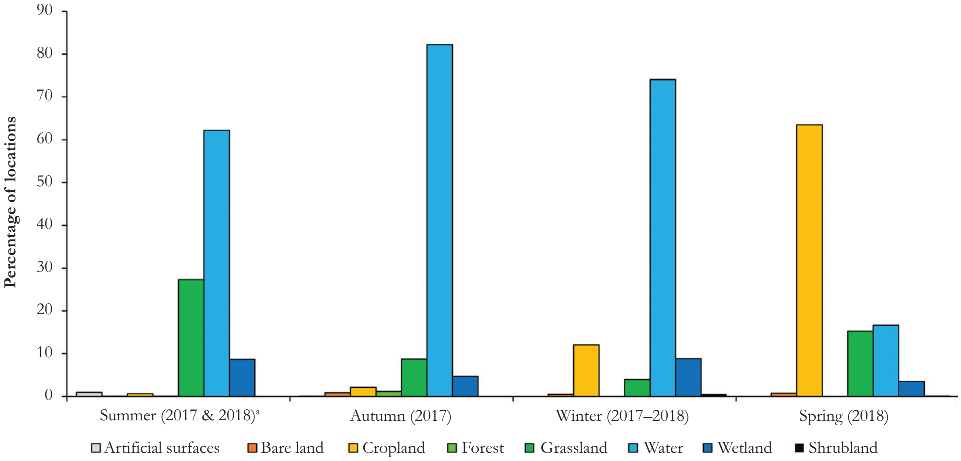

Figure 6. Land use classification types at sites used by Whooper Swans tracked throughout the spring, summer, autumn and winter periods from 2017–2018 which wintered in China. Data are derived from GPS fixes generated by nine birds caught in summer in Western Mongolia in 2017 overlaid upon land cover maps from 2017 (Gong *et al.* 2019). In summer 2017 and 2018, Whooper Swans (9 individuals, mean ± s.d. = 3,903 ± 2,164 fixes per site) used water (62.2%), grassland (27.3%) and wetland (8.7%) habitats. In autumn 2017, Whooper Swans (7 individuals, 11 stopover sites, 264 ± 181 fixes per site) used water (82.2%) and grasslands (8.8%). In winter 2017/18, Whooper Swans (9 individuals, 2,692 ± 474 fixes per site) used water (74.1%), cropland (12.0%) and wetland (8.8%). In spring 2018, Whooper Swans (5 individuals, 13 stopover sites, 422 ± 172 fixes per site) mainly used cropland (63.5%), water (16.7%), grassland (15.3%), and bare land (0.8%). [a]summer data in 2017 was from the day after the birds were captured to the day before the autumn migration; the summering data in 2018 was incomplete for three out of five individuals: two individuals (ws005, ws008) provided complete data, two individuals (ws001, ws002) lost contact and one individual (ws006) died during the summer period.

cropland (63.5%) was the most commonly used land use type at stopover sites, followed by water (16.7%) and grassland (15.3%, Fig. 6). No tracking fix was within a protected area (Fig 7, Table 6).

Discussion

Distribution of the East Asian population

For the first time, we integrated satellite tracking data, survey data, ring resightings and expert knowledge to summarise our understanding of the distribution and migration of the Whooper Swan in East Asia. Xinjiang, Qinghai and Gansu Provinces and Beijing City in China were identified as new wintering areas (Fig. 1, Fig. 2). Some exchange was detected between Chinese- and Korean-wintering populations: one bird moved from South Korea to China in the same winter (Fig. 2), and five Whooper Swans which summered in western Mongolia flew to South Korea or China (Newman *et al.* 2009).

We should be very careful not to draw too many conclusions from the results,

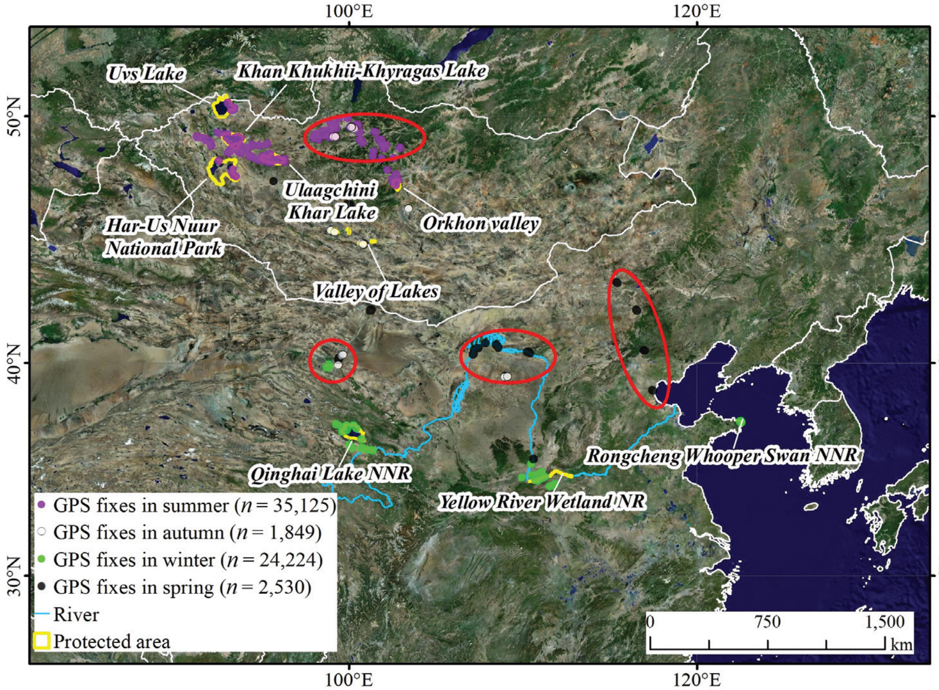

Figure 7. Use of protected areas by nine tagged Whooper Swans, which bred in Western Mongolia and wintered in China between 2017 and 2018. The analysis is based on GPS fixes during autumn 2017 (7 individuals, 11 stopover sites, mean ± s.d. = 264 ± 181 fixes per site), winter 2017 (9 individuals, 2,692 ± 474 fixes per site), summer 2017 and 2018 (9 individuals, 3,903 ± 2,164 fixes per site) and in spring 2018 (5 individuals, 13 stopover sites, 422 ± 172 fixes per site). Yellow borders indicate the protected areas Whooper Swans occupied, identified by name in white text. Red circles highlight areas of potentially high importance as staging areas that should be investigated as potential protected areas (the Arkhangai region in Mongolia and the Heihe region, the bend of the Yellow River and the northern part of north China) highlighted by this study.

because of the highly biased and limited geographical nature of the capture sites of tracked individuals and of the resighting effort, which greatly skews our knowledge, totally omitting Whooper Swans breeding in the extreme Far East, for example (Fig. 2). We remain ignorant of the distribution and abundance of the Whooper Swan throughout much of its vast summer range in East Asia.

Although we found 35 birds faithful to their wintering site, compared to one bird that moved between Chinese and South Korean wintering areas, levels of philopatry require regular reports of colour-marked birds from their breeding and wintering areas and/or data from more telemetry tagged birds to avoid observation bias. This is especially the case when assessing winter site fidelity from reports of birds identified

Table 6. Conservation status of sites used by nine Whooper Swans which bred in Western Mongolia and wintered in China between 2017 and 2018, based on GPS fixes recorded during the autumn stopover period in 2017, the wintering period in 2017/2018 and the spring stopover period in 2018.

Season	Total no. of fixes	No. of fixes within protected areas	Percentage in protected areas	Protected areas occupied
Summer, 2017 & 2018[a]	35,125	16,482	46.9%	Har-Us Nuur National Park; Khan Khukhii-Khyragas Lake; Orkhon valley; Ulaagchini Khar Lake; Uvs Lake
Autumn stopovers, 2017	1,849	471	25.5%	Valley of Lakes (Boon Tsagaan Lake, Taatsiin Tsagaan Lake, Adgiin Tasgaan Lake, Orog Lake)
Winter, 2017/18	24,224	8,543	35.3%	Qinghai Lake, Yellow River Wetland, Rongcheng Whooper Swan National Nature Reserve
Spring stopovers, 2018	2,530	0	0.0%	–

[a]The summer data in 2017 were from the day after the birds were captured to the day before the autumn migration; the summer data in 2018 were incomplete for three out of five individuals: two individuals (ws005, ws008) provided data for the whole summer, two individuals (ws001, ws002) lost contact and one individual died (ws006) during the summer period.

by their neck-collar codes, because observers tended to visit the same sites and resight the same birds in successive periods. Whooper Swans ringed in Iceland show variable levels of winter site fidelity (*e.g.* Newth *et al.* 2013 and references therein).

Abundance estimates and trends in the East Asian population

In China, South Korea and Japan, the number of wintering swans has increased during 1970 to 2019 (Fig. 3). Numbers of swans recorded wintering in China were much higher in 2019 compared to annual totals going back to 1988–1993 (Fig. 3). This was very likely the result of improved survey coverage in 2019, although it may also result from genuine increases in the population size, potentially aided by the increase in supplementary feeding in protected areas, which is known to attract Whooper Swan aggregations locally. In the Rongcheng Whooper Swan Reserve in Shandong Province, 250 kg corn and cabbage have been provided every day since 2009 and in Sanmenxia Wetland Park in Henan Province, 150 kg corn and cabbage have been provided twice a day since January 2009.

The East Asian population estimate of 57,690 individuals generated in this study is close to the estimate of 60,000 individuals by Wetlands International in the end of the 20th century (Miyabayashi & Mundkur 1999; Wetlands International 2019). We consider this population estimate reliable, because the counts of Whooper Swans in Japan and South Korea covered the distribution of this species well, and the counts of Whooper Swans in China covered the seven provinces which constitute the main wintering areas. However, some sites which may be temporarily important for the species might have been missed, such as the Yuyang River Swan Nature Reserve, Shaanxi Province, where 600 Whooper Swans were counted on 18 November 2019 (Xin Wang, pers. comm.).

Key wintering sites in China that exceeded 1% of the total population size for the East Asian Whooper Swan population (*i.e.* a criterion for identifying sites of international importance) between 2012 and 2019 were located in Xinjiang Uygur Autonomous Region, Qinghai, Henan, Shanxi, and Shandong Provinces (Fig. 4). While we lack tracking data from Whooper Swans using the Xinjiang Uygur Autonomous Region, other key wintering sites have supported tracked individuals that tell us about their summer provenance and migration routes. The telemetry tracks from Whooper Swans showed that the main stopover sites in autumn were restricted to some lakes in central and Western Mongolia, the Heihe River in Gansu Province and the Yellow River in Ordos city in Inner Mongolia. Spring migration stopover sites were mainly concentrated in the Heihe River in Gansu Province, Jizikou of the Yellow River, Beidagang and Zhangjiakou. The collar resightings data showed that these individuals used similar key wintering sites to those used by the tagged birds, except for one site in Xinjiang Province. This implies that there might be other Whooper Swans breeding elsewhere in currently unknown areas, which winter in the Xinjiang Uygur Autonomous Region in China, and in South Korea.

Comparison of migration parameters in spring and autumn migrations

It is generally the case that in many avian species, earliest arriving individuals breed earlier with greater reproductive output of better quality young than birds arriving later (Kokko 1999). In contrast, there is less incentive for early arrival and reduced limitations on time for birds reaching the wintering grounds, so birds on autumn migration are more likely adopt a strategy to minimize energy (van Noordwijk *et al.* 1995; Kokko 1999; Greenberg & Marra 2005). It is therefore hypothesised that pre-breeding (spring) migration will be more time constrained than the post-breeding (in autumn) migration, predicting faster migration in spring than in autumn (Nilsson *et al.* 2013). Migratory swans have a short window of opportunity to nest, hatch and fledge young in their annual cycle (Rees *et al.* 1996; Boiko *et al.* 2014) and, being highly territorial during the breeding season, pre-breeding (spring) migration is likely to be highly time constrained, because of strong competition to arrive early to breeding areas to secure and reoccupy breeding territories (Kokko 1999). Hence, it was expected that spring migration of East Asian Whooper Swans would be faster than autumn. In fact, this study found that the spring migration was slower than that in autumn (Table 5), in contrast to general theory and expectations. However, this is similar to a study of Bewick's Swan migration across northwest Europe, which found that ringed birds were more frequently resighted in spring than in autumn, with one suggestion being that the birds move more rapidly to their intended wintering sites (Evans 1982). Seasonal differences in food availability, wind conditions (Shamoun-Baranes *et al.* 2003), patterns of snow and ice melt along the flyway (Bauer *et al.* 2006; Nuijten *et al.* 2014; Li *et al.* 2020) all conspire to affect the timing and speed of the spring migration of individual large waterbirds and therefore, in all likelihood, Whooper Swans.

Land use type and conservation status at stopover sites

Whooper Swans that migrated from Mongolia to China showed a high probability of using areas of open water in summer, autumn and winter, likely because the species traditionally feeds on aquatic vegetation (Haapanen *et al.* 1977; Rees *et al.* 1997; Jia *et al.* 2019). They used lakes of all sizes in the Gobi Desert of Mongolia, wetlands in the middle reaches of the Yellow River and small lakes in Inner Mongolia. Consistent with previous findings, Whooper Swans often used lakes and estuarine deltas at stopover sites, and freshwater lakes, swamps, saltwater lagoons and bays during winter (Owen *et al.* 1986). Interestingly, swans occurred on croplands in almost two-thirds of all positional fixes in spring. It has been shown that the energy and nutritional content of most agricultural crops are as great, or greater than, the natural foods of wild geese and by virtue of high energy density and often mono-specific stands offer highly profitable feeding opportunities (Fox & Abraham 2017). Over the past 50 years, Whooper Swans have similarly increasingly used croplands in the vicinity of waterbodies (which provide a safe roost) as their winter habitat in northwest Europe (Laubek *et al.* 1999, 2019;

Robinson *et al.* 2004; Hall *et al.* 2016) and also more recently in China (Dong *et al.* 2007). In this study, cropland was also intensively used in spring, which probably supports the hypothesis that use of agricultural landscapes helps to improve intake rate of energy and nutrition and potentially enhance reproductive output (Fox & Abraham 2017).

The relatively high percentages of swan positions from within protected areas in summer and winter, 46.9% and 35.3%, respectively, suggests that nature conservation site safeguard programmes currently provide reasonable levels of protection for the species during these two periods of the annual cycles. The Mongolian plateau summering areas are both adequately protected and little disturbed by humans and some of the nature reserves at Chinese wintering sites have attracted Whooper Swans by supplementary feeding and enhanced public interest in the species. However, no spring stopover sites were located in protected areas (Fig. 7, Fig. 8), while 25.5% of autumn stopover sites were

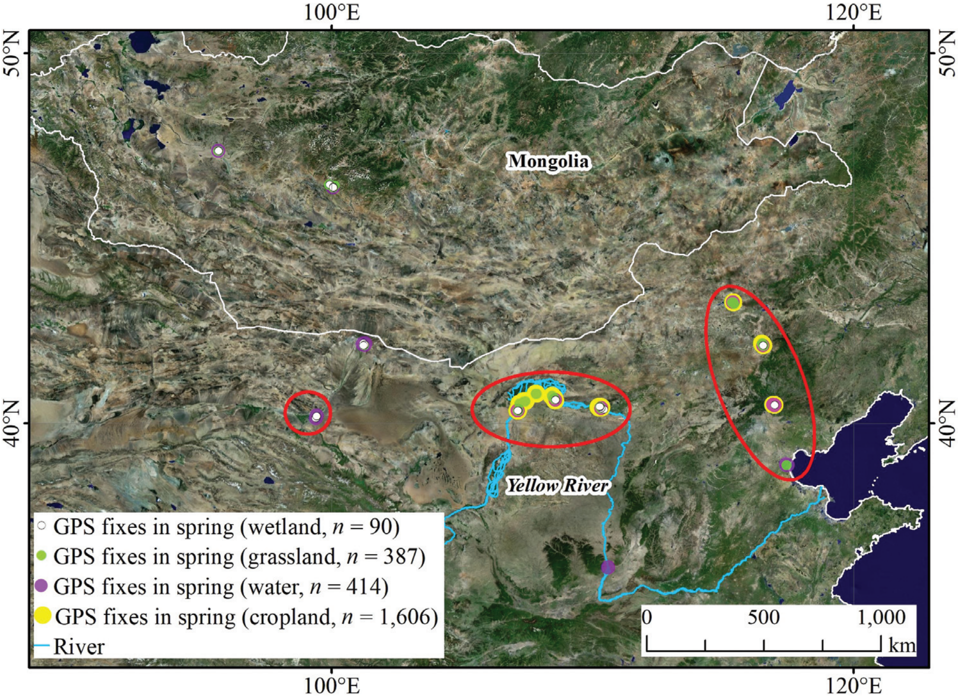

Figure 8. Spring stopover sites of potential importance for Whooper Swan (based on 5 individuals, 13 stopover sites, mean ± s.d. = 422 ± 172 fixes per site) identified during spring 2018. The white symbols indicate sites where the GPS fixes suggest swans were using wetland, green symbols grassland, purple symbols water and yellow symbols cropland. The red circles identify the areas we recommend should be investigated for designation of future protected areas for the species (Heihe region, the bend of the Yellow River and areas in northern China) based on the results from this study.

in protected areas, suggesting there is inadequate protection of sites used by this species during migration stopover periods. The limited number of tracked birds made this pattern difficult to interpret and restricted our ability to identify specific conservation gaps for the species, but these results suggested more conservation effort should be put into protecting sites of critical importance used by this species during its annual cycle. This is because the declined fitness resulted from the lack of conservation in one stage, may influence performance in subsequent life stages, *i.e.* carry-over effects (Norris 2005).

Recommendations for research and conservation

The pressures of land reclamation, resource development, hydrological change and pollution threaten wetlands across the world, including in the East Asian region. Current climate change predictions also indicate an increasing pressure on wetlands, mainly due to hydrological changes, and to temperature and sea level rises (Junk *et al.* 2013). Overgrazing, disturbance and other threats from human activities are thought to be having an adverse effect on the abundance of Whooper Swans wintering in China (Ma & Cai 2000, 2002). China therefore has established nature reserves, *e.g.* at Wuliangsuhai in Inner Mongolia, Rongcheng in Shandong, Sanmenxia in Henan and Bayanbulak in Xinjiang, mainly to protect Whooper Swans and their habitats. A series of measures, including artificial feeding and wetland restoration, have been implemented to protect the extent and quantity of waterbird habitats more widely, but especially for the swans (State Forestry and Grassland Administration of China 2019).

Establishment of a coordinated long-term continuous and standardised monitoring programme on the winter quarters (especially in China) would lead to a better understanding of changes in species distribution and abundance at a suite of key sites, thus providing a sound scientific basis for advising effectively on the protection and management of the habitat needed for sustaining the Whooper Swan in East Asia. Closer international collaboration on monitoring, research and management should combine telemetry data with within-site distributional count data to determine the causes of between-site movements in relation to food profitability and availability, in order to guide habitat management plans. This would help to develop targeted conservation strategies at site, regional and flyway levels for this species. Use of remote sensing tools currently available, combined with greater sample sizes from telemetry studies, provide exciting prospects for future, deeper investigations of the relationships between landscape features and the speed and nature of the Whooper Swans' migrations, not only for this East Asian population but throughout Eurasia. The importance of protecting habitat used by the swans throughout the year is highlighted, together with the need for more surveys and tracking studies to understand the distribution, status and ecology of this species. Extensive telemetry studies in particular should be continued to identify important habitats and conservation gaps for the Whooper Swan in East Asia. We also recommend more investment in public education to improve citizens' scientific literacy, which should help to promote not only current but future protection of wetland sites and migratory birds, thus enhancing efforts to maintain Whooper Swans (and other migratory birds) in the Far East Asian flyway.

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Photograph: Whooper Swans on a misty morning, by Takeshi Kino/WWT.