The migratory Mute Swan *Cygnus olor* population in East Asia

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Abstract

Until recently, almost nothing was known about the migration routes, flyway structure and population status of the Mute Swan *Cygnus olor* in East Asia. Here, we use a combination of GPS telemetry data, collar resightings, published literature and expert advice to update existing knowledge of its summer and winter distribution in the region, and to provide a preliminary description of the swans' migration and habitat use. Three flyway units were indicated for the Mute Swan in East Asia. The Eastern China-wintering unit includes swans summering along the lower Selenga River in Russia, in central Mongolia and Inner Mongolia in China, which winter on the coast of eastern China, where 403 swans were recorded in 2014/15 but where fewer than 30 have been counted in very recent years. In the absence of better data, we conservatively estimate this Chinese-wintering group at 400 birds. Mute Swans in the Korean-wintering unit are individuals that winter along the Korean Peninsula and summer in Inner Mongolia (China) and the Amur region (on the border of China and Russia); they are poorly covered by the mid-winter waterbird counts in South Korea and we have no knowledge of numbers wintering in North Korea. Finally, mid-winter counts of the introduced and sedentary population of Mute Swans in Japan have amounted to *c.* 240 birds in the last five years. We therefore suspect that there are likely *c.* 1,000 Mute Swans in Far East Asia, but await improved coverage throughout the entire wintering grounds to provide a better population estimate, with the species confirmed as one of the poorer known of the migratory waterbirds in the region. A single GPS-tagged Mute Swan tracked successfully provided detailed information on its migration routes, timing of migration and habitat use (almost exclusively waterbodies) over four complete migration episodes. It summered at Dalai Lake, China, used three stopover sites (on the borders of Russia and North Korea, in North Korea, and Baicheng City in China) during spring and autumn migration, and showed site fidelity to summer, winter and stopover sites. Combined count data and GPS data suggested that Mute Swans mostly occur within protected areas throughout the year. However, further research is required to establish the true distribution and abundance of this small and scattered species within these three flyways in East Asia, as well as to confirm its population structure and migration routes.

Key words: abundance, *Cygnus olor*, East Asia, habitat use, migration routes, Mute Swan, site fidelity, telemetry.

The Mute Swan *Cygnus olor* is the most abundant of the swan species, with a total of seven populations distributed around the world, in total comprising > 600,000 individuals (Rees *et al.* 2019; Wetlands International 2019). It is also the best-studied of all of the swans, with more research undertaken than on any of the other true swans *Cygnus* sp. (Wood *et al.* 2019a). To date, however, almost all of our knowledge of the Mute Swan has been obtained from studies undertaken in Europe or North America (Birkhead & Perrins 1986; Wood *et al.* 2019b; Gayet *et al.* 2020). In contrast, the East Asian population has received little attention and so remains poorly understood. Its population size was most recently estimated at 1,000–3,000 birds (Wetlands International 2019), including two migratory groups (a Northeast China–Korean Peninsula group, and a Mongolia & Northern China–Eastern China group), and with an introduced population of some 200–300 birds (up to 367 in 2017) resident in Japan (Rees *et al.* 2019; Carboneras & Kirwan 2020; Gayet *et al.* 2020). The distribution, migration routes and behaviours were largely unknown or undocumented, except for scattered sites used as wintering, breeding and stopover areas, although Inner Mongolia was known to be an established summering area and a stopover site for this population (Zhao *et al.* 2008). Every year from mid-March to early April, Mute Swans migrate to Inner Mongolia, remaining until November (Zhao *et al.* 2017). At Ulansu Lake in Inner Mongolia, identified as a major breeding and stopover site for the species in China, maximum autumn numbers reached 1,300 in 2004, although peak numbers fluctuated widely from 2–1,060 between 1996–2007 (Zhao *et al.* 2019).

Chinese-wintering Mute Swans are distributed mainly along the coast of Shandong, and Cao *et al.* (2008) estimated that *c.* 650 spend the winter in the country.

Information on their overall distribution and use of particular sites however remains patchy, despite such information being a fundamental prerequisite for the conservation and management of the East Asian Mute Swan population, not only within China but throughout its range. Mute Swans are known to be sensitive to environmental perturbations, such as oil pollution, lead poisoning or habitat degradation (Minton 1971; Wood *et al.* 2019b; Zaynagutdinova *et al.* 2019), and yet such impacts cannot be addressed without knowledge of swan numbers, distribution and seasonal movements.

In this study, we attempt to update our knowledge of the geographical extent of the summer and winter ranges of the migratory Mute Swan in East Asia, investigate their migration routes and provide a better assessment of population size, based on a combination of collar resightings and telemetry, waterbird surveys, birdwatching archives and expert knowledge.

Methods

Migration data

Five flightless Mute Swans were captured on their summering areas: one female adult caught by hand at Dalai Lake, China (48.36°N, 117.53°E) in September 2016, and four individuals (two male juveniles and two female adults) caught with hand nets from boats while moulting at Buir Lake, Mongolia (47.67°N, 117.58°E) in July 2017 (Fig. 1). The birds were fitted with two types of solar-powered GPS loggers mounted on neck collars (Druid Tech, China, 45g, and KoEco, Republic of Korea, 103g; both constituting < 2% of total body mass; Supporting Materials Table S1), which recorded GPS positions and transmitted data via the GSM mobile telephone networks. The standard cycle for recording GPS positional fixes varied from one fix per hour to one fix per day, depending on transmitter type and battery condition. On average, the Druid transmitter provided 21 ± 4 (mean ± s.d., range = 1–25) GPS positions per day, and the KoEco transmitter 8 ± 2 (range = 2–12) GPS positions per day, contingent upon power supply. Positional accuracy was found to be within a mean of 12.5 m (± 4.7 s.d. based on 17 static loggers and 1,186 fixes) for Druid loggers and 13.8 m (± 6.8 s.d. from 48 static loggers and 2,539 fixes) for KoEco devices. First-day movement data after the birds were captured and last-day data before a bird died or lost contact, were excluded from all analyses. Three KoEco transmitters failed to return GPS fixes, but were resighted in the field during migration, and individuals were identified by the code engraved on the neck collar (Supporting Materials Table S1). These sightings were also used in describing the migration routes.

Distribution, migration range and key sites

The Mute Swans' distribution was initially delineated in ArcGIS 10.2 (ESRI 2013) based on the map previously generated by BirdLife International and Handbook of the Birds of the World (2019). Historically archived bird-watching records (*e.g.* counts from China, South Korea, North Korea, Japan, Mongolia and Russia entered into eBird; Cornell Lab of Ornithology 2020),

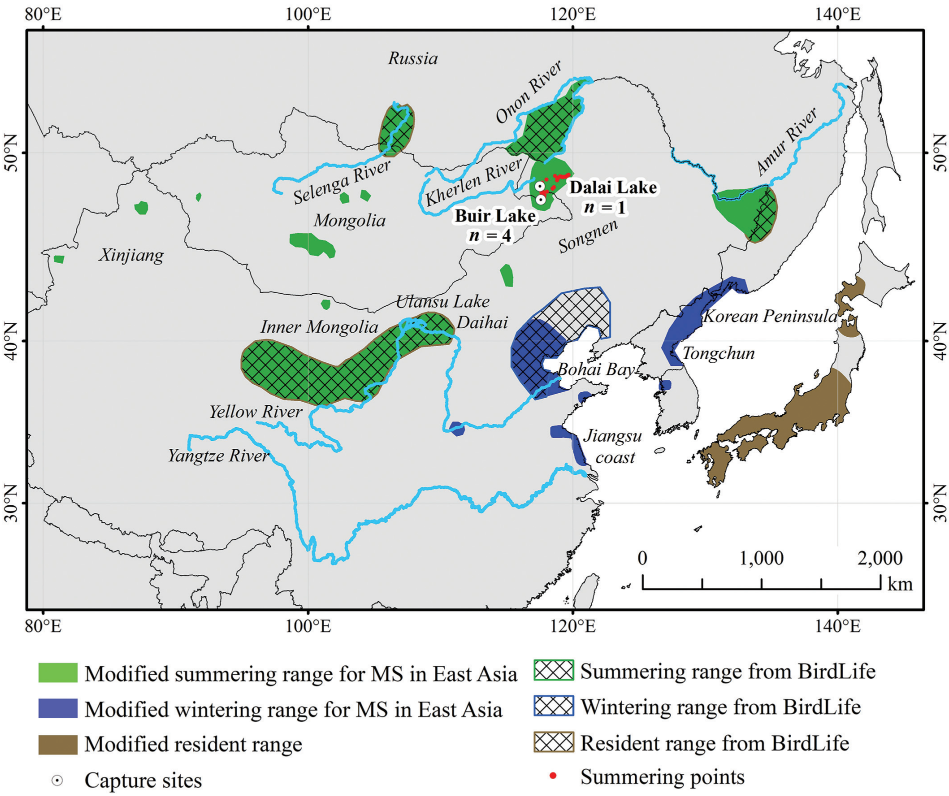

Figure 1. Revised distribution map for the Mute Swan in East Asia. Summering areas (shaded in solid green) are mainly in the lower reaches of the Selenga River (Russia), central Mongolia, Inner Mongolia (China), and the Amur River region on the Chinese-Russian border. The wintering range (shaded in blue) is primarily also the coast of eastern China and on the Korean Peninsula. Mute Swans in Japan (shown in brown) comprise an introduced resident population. The map is modified from the distribution illustrated in BirdLife International and Handbook of the Birds of the World (2019), with the revised range based on birdwatching records in eBird (Cornell Lab of Ornithology 2020), compiled field surveys and literature (Supporting Materials Table S2), expert knowledge, and tracking data (see *Methods* for details). Red dots = GPS locations recorded between the first arrival and last departure dates for the tagged individual in its summering area. Five individuals were caught at two sites in summer, at Dalai Lake and Buir Lake) cross summering ranges in East Asia. Dot-centred circles = capture sites; *n* = number of birds caught. All the sites/areas mentioned in the paper are shown on the map.

satellite tracking data (Supporting Materials Table S1), field survey results and published count data compiled by the authors (Supporting Materials Table S2) and expert knowledge were then combined to reassess the distribution, migration routes and key sites used by the Mute Swan in East Asia. Because this species was not subject to regular and systematic monitoring before the year 2000, we have excluded counts from China before that year, so the results presented here reflect its current status and distribution. In order to eliminate possible irregular observations (*e.g.* misidentification) involved in the birdwatching records, counts were excluded if: 1) they were outside the range illustrated in BirdLife International and Handbook of the Birds of the World (2019), and 2) there were no other Mute Swans counted within a 100 km radius of the observation point in the same/adjacent seasons in other years. In this study, spring was defined as being from 1 March to 15 April, summer from 16 April to 15 October, autumn from 16 October to 30 November, and winter from December to February, which was informed by the activity patterns revealed by the tracking data. While this definition may not delineate the annual cycle of the Mute Swan precisely, it did allow us to capture the broad trends in seasonal movements, where present. Key sites were classified as being those that at least once exceeded 1% of the East Asian population estimate (*i.e.* 30 individuals; Wetlands International 2019) from the year 2000 onwards.

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, six experts from three countries discussed and updated delineation of the distribution and migration routes followed by the Mute Swan in the East Asian flyway (Appendix 1).

Migration parameters

The main areas used by the tracked individual in summer, during migration and on the wintering grounds were determined from the GPS data. These GPS fixes were also used to determine the flight/non-flight status of the bird (*i.e.* whether moving between sites or commuting within a site), and thus to distinguish between the start and end dates of spring and autumn migration episodes, and the timing of arrival/departure at breeding and wintering sites (following the method of Wang *et al.* 2018b). Migration duration was calculated as the time that a Mute Swan took to travel between the summering site and wintering site, including time spent at any stopover sites during the journey. Any site at which the bird stopped for > 48 h was defined as a stopover site (Kölzsch *et al.* 2015), and the number of stopovers was calculated accordingly (Wang *et al.* 2018a). Stopover duration was calculated as the sum of the days spent at each stopover site during each migration season, and the days actually spent travelling (total travel days) was determined for each bird as the total migration duration minus any stopover duration. A flight leg was defined as a journey connecting subsequent stopover, wintering or summering sites, to generate the number of flight legs involved in each spring/autumn migration episode. The mean step length was calculated as the migration distance divided by the number of flight legs during each migration season. Migration distance was the cumulative distance travelled between wintering and summering sites. Thus, the migration/travel speed can be calculated as the migration distance divided by the migration duration/total travel days. A straightness index was calculated for each complete migration as the straight-line distance between the last departure and first arrival locations, divided by the total migration distance actually taken along the path followed by that individual bird (Benhamou 2004).

Home range, habitat use and movements during the summer, winter and stopover periods

The sizes of the home ranges recorded for the Mute Swan tracked during different stages of migration (in winter, summer and at stopover sites) were calculated as the 50% (core area) and 90% (overall home range) utilisation distribution (UD), using the fixed Kernel Density Estimation (KDE) method (Seaman & Powell 1996). KDE was calculated using the package "adehabitat" (Calenge 2006) in Program R 3.6 (R Core Team 2019) and mapped in ArcGIS 10.2 software (ESRI 2013).

Habitat use (in winter, summer and at stopover sites) was analysed by overlaying the positions used by the Mute Swan upon the land cover layers identified in 2017 at a resolution of 10m × 10m (Gong *et al.* 2020). Habitats were grouped into 10 different categories, which comprised cultivated land, forest, grassland, shrubland, wetland, water bodies, tundra, artificial surfaces (*i.e.* the built environment), bare land (which may include bare mud, as well as rock and other bare substrate), and snow/ice. The area of each habitat within the home ranges was calculated using ArcGIS 10.2 (ESRI 2013), with habitat use during the different time periods (at summer, winter and stopover sites) measured as the GPS locations recorded for the tracked individual. We defined a "Centroid location" for wintering, summering and stopover sites as the location with the average longitude and latitude of all locations during these periods in different years, to assess the level of site loyalty and movement between years.

The daytime, night-time and overall daily movement (Abdlrahem & Sherwali 2009) of the tracked individual was calculated as the accumulated distance of adjacent GPS locations during each period of the day. Daytime was defined as being from 1 h before local sunrise until 1 h after sunset, because birds often move in twilight (for an example in swans, see Pennycuick *et al.* 1999). The sunrise and sunset time at the swan's location on each date was calculated using the "suncalc" package in R (Thieurmel & Elmarhraoui 2019).

Abundance estimates and trends

Because of the lack of regular systematic surveys in China, Mute Swan abundance in the country was estimated by aggregating count data from three sources: 1) winter counts (December, January and February) recorded during waterbird surveys, 2) a literature review, and 3) unsystematic birdwatching counts (Supporting Materials Table S2). Duplicate counts from the same sites were removed, such that only the maximum counts were used in the abundance estimates. We acknowledge that this approach may be inaccurate because it missed some sites in one year and others in another year. However, the accumulated data provides an approximate estimate of the situation, against which future methods can be refined.

The Korean Ministry of Environment and its associated institutes, National

Institute of Environmental Research (until 2007) and the National Institute of Biological Resources (since 2008), annually conduct a nationwide census at most lakes, reservoirs, lengths of seashore and bays known to be important for waterbirds during the non-breeding period. The simultaneous two-day field counts are coordinated annually in mid- or late January by ornithologists, experienced birdwatchers and volunteers to estimate the distribution and abundance of wintering waterbirds in South Korea.

In Japan, an annual census of waterfowl (Anatidae) species has been conducted by the Ministry of the Environment, with the assistance of prefectural governments, in mid-winter (*c.* 15 January) each year since 1970 covering all principal sites for swan, goose and duck species throughout the country during the non-breeding season (Ministry of the Environment of the Government of Japan 2019). As an introduced species, Mute Swan was only included in the census from winter 1987/88 onwards.

Initial exploration of linear regression residuals of temporal trends in the China count data (where most of the migratory East Asian Mute Swans were recorded), fitted using the nlme package (Pinheiro *et al.* 2020), showed only minor evidence of statistically significant residual temporal autocorrelation (at time lag 6); for all other time lags there was no indication of temporal autocorrelation ($P > 0.05$, n.s.). Given the lack of serial residual autocorrelation, no autocorrelation structure was included in subsequent linear regression analyses.

Results

Distribution, migration routes and key sites

Data obtained during this study indicated that Mute Swans in East Asia currently occur mainly in eastern Mongolia and in the Inner Mongolia region of China during summer, whilst the wintering areas are primarily along the coast of eastern China and on the Korean Peninsula (Fig. 1). In the lower reaches of Selenga River, Inner Mongolia and the Amur River region on the Chinese-Russian border, Mute Swans had previously been considered as resident throughout the year (BirdLife International and Handbook of the Birds of the World 2019). However, on the basis of local knowledge, these areas have been reidentified as breeding areas for Mute Swans migrating elsewhere in winter. A combination of counts and expert knowledge suggests that delineation of the swans' summer distribution should be expanded to include wetlands in the lower reaches of the Kherlen River in Mongolia and Inner Mongolia. The winter distribution was realigned in the Bohai Bay region and extended to include the Jiangsu coast of China, the northeast coast of North Korea and the western coast of South Korea.

Between summer 2016 and spring 2018, we collected: 1) four complete migration routes for swan MS001, from 26 September 2016 to 13 April 2018, 2) an incomplete autumn migration for swan MS002 in 2017, and 3) two sites where individuals MS003, MS004 and MS005 were resighted in the field (Fig. 2). Swan MS001 followed a route

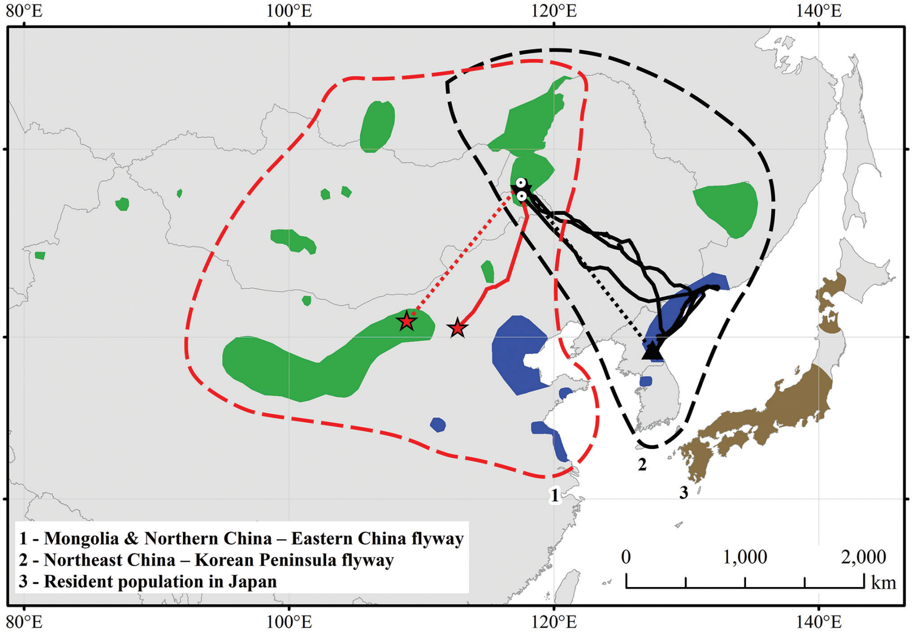

Figure 2. Preliminary assessment of flyways used by the Mute Swan in East Asia: 1) the Mongolia & Northern China–Eastern China flyway (red dashed line; birds mainly summered in the lower reaches of the Selenga River, Russia, in central Mongolia, and in Inner Mongolia, China, and winter on the eastern coast of China); 2) the Northeast China–Korean Peninsula flyway (black dashed line; birds summered in Inner Mongolia, China, and the Amur River region on the Chinese-Russian border, and winter on the Korean Peninsula); and 3) the resident population in Japan (shown in brown). Information on the flyway ranges are based on birdwatching records in eBird (Cornell Lab of Ornithology 2020), count data compiled from field surveys and a literature review (Supporting Materials Table S2), expert knowledge and tracking data (see *Methods* for details). Swans from the Mongolia & Northern China – Eastern China flyway included two birds caught at Buir Lake, western Mongolia, which were resighted at Ulansu Lake and Daihai in Inner Mongolia (red stars), most likely a stopover site. One of these had an incomplete migration (red solid line); the other lacked detailed migration data (red dotted line). The Northeast China–Korean Peninsula flyway included one bird caught at Dalai Lake, which summered in Inner Mongolia, China, and wintered on the Korean Peninsula, and provided data for three complete migrations (dark solid lines). Two more birds caught at Buir Lake, were resighted in Tongchun, North Korea (dark dotted line). Summer, winter and resident (year-round) ranges are shaded in green, blue and brown, respectively. Dot-centred circle = the capture sites. The black inverted and regular triangles = summer and wintering sites, respectively, of tracked individuals.

through Northeast China and the Korean Peninsula. This individual, which summered in the Buir Lake area on the border between China and eastern Mongolia, migrated across the Songnen Plain in northeast China to winter on the coast of Russia and North Korea (Fig. 2). We defined a second flyway (Mongolia & Northern China–Eastern

China) based on field observations of Mute Swans reported along the route (Fig. 3). Birds breeding in northern China and Mongolia almost certainly winter in eastern China, because of the relative proximity of this wintering area and the lack of records of Mute Swans wintering elsewhere between the two regions, but further telemetry work is required to confirm that this is the case.

Seasonal variation in Mute Swan numbers, or simply presence/absence, evident across East Asia (in China, Mongolia, South Korea, North Korea and Russia) in the field surveys, birdwatching websites and literature review, indicated a clear pattern of seasonal migration (Fig. 3). In summer, the birds were located mainly in Mongolia, Inner Mongolia and in Xinjiang, China, during which period no swans were seen in eastern China. In contrast, no swans were reported from their summer range during the winter, when all counts showed Mute Swans to aggregate on the east China coast and the Korean Peninsula, in areas where no birds were counted during the summer. Unfortunately, we lack counts from North Korea, where our one tagged bird overwintered, confirming the presence of unknown numbers of Mute Swans wintering in this country. Counts in spring and autumn came from areas situated between these winter and summer ranges. The Mute Swans' distribution in Japan was stable across seasons, reinforcing the view that it is a resident, non-migratory population.

Abundance estimates

The counts and tracking data thus suggest that the migratory Mute Swans in East Asia follow two flyways, with little or no interchange with a third element, the introduced population resident in Japan, although we lack multiple telemetry data to confirm these patterns. Numbers wintering in China, showed no clear population trends from 2004 to 2020 (P = 0.37, n.s.; Fig. 4A), probably due to lack of systematic continuous and synchronous surveys. After a single count of 403 in 2014/15, winter surveys conducted during the last five years have only recorded up to 21 individuals (Fig. 4A). Key wintering sites noted between 2009/10–2019/20 included the Yellow River delta and Beidagang, with the Yellow River delta, Tian'e Lake and Dingziwan important for the species before 2009/10 (Fig. 5). Very few Mute Swans winter in South Korea (Fig 4A), but it is thought that the surveys do not cover the entire area used by the species in this country. It is assumed that the numbers wintering there are greater than the maximum count of 29 (in 2002), so it is likely that many Mute Swans are missed here and especially in North Korea, where we lack counts but are aware that the species winters. The non-migratory Mute Swan population in Japan is currently estimated to number some 240 birds, based on assessments from 2015/16–2019/20 inclusive (Fig. 4B; Supporting Materials Table S3).

Migration patterns

The tagged swan MS001 began its autumn migration at the end of October, covering a distance of 1,735 km within 32 days in autumn 2016, and 2,105 km within 30 days in autumn 2017 (Table 1). During spring migration, the bird departed 12 days later in 2018 than 2017, and used one more

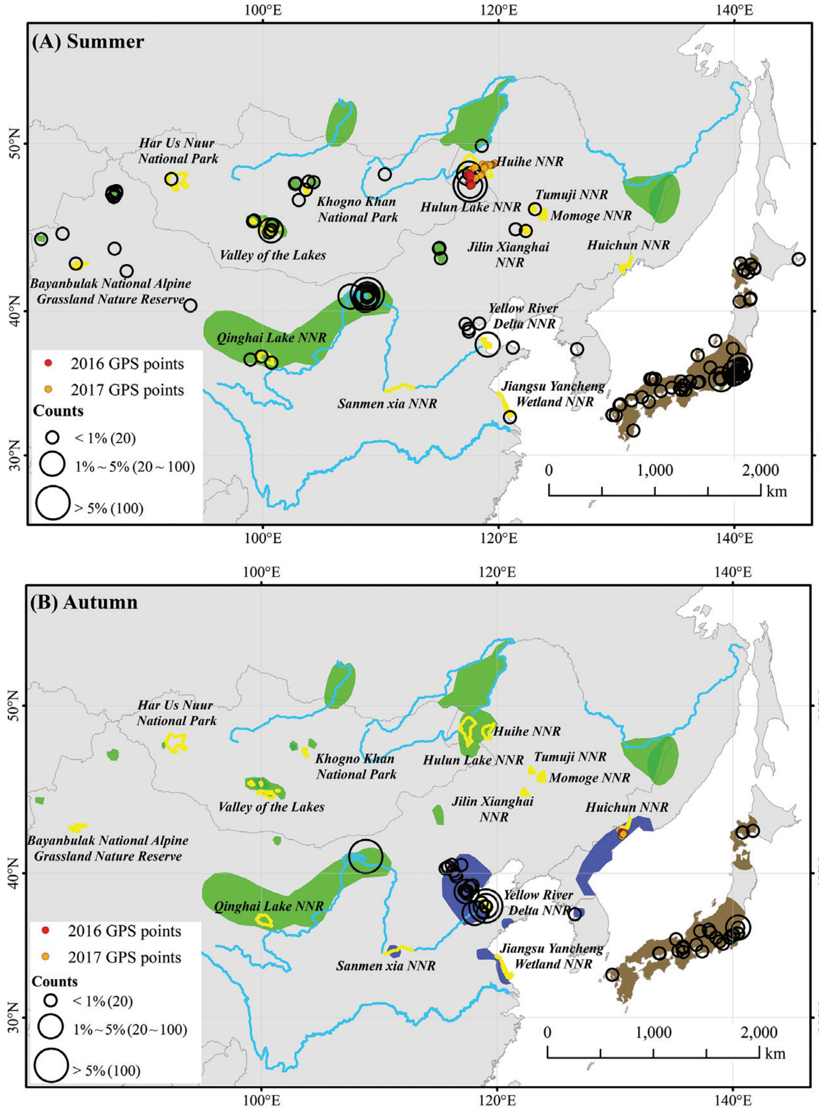

Figure 3. Location of Mute Swan records (counts and GPS tracking data) in relation to season and protected areas. (A) Summer = 16 April–15 October; (B) Autumn = 16 October–30 November; (C) Winter = 1 December–end February); and (D) Spring = 1 March–15 April. Counts were derived from eBird (Cornell Lab of Ornithology 2020), field surveys by the authors and a literature review of records reported since 2000 (Supporting Materials Table S2). The 1% (20 birds) and 5% (100 birds) levels used to determine sites important for the species are based on the population estimates for Mute Swans in East Asia (Wetlands International 2019). Seasons were divided according to the tracking data (see *Methods* above). GPS points were for the Mute Swan tagged MS001, tracked from summer 2016 to spring 2018.

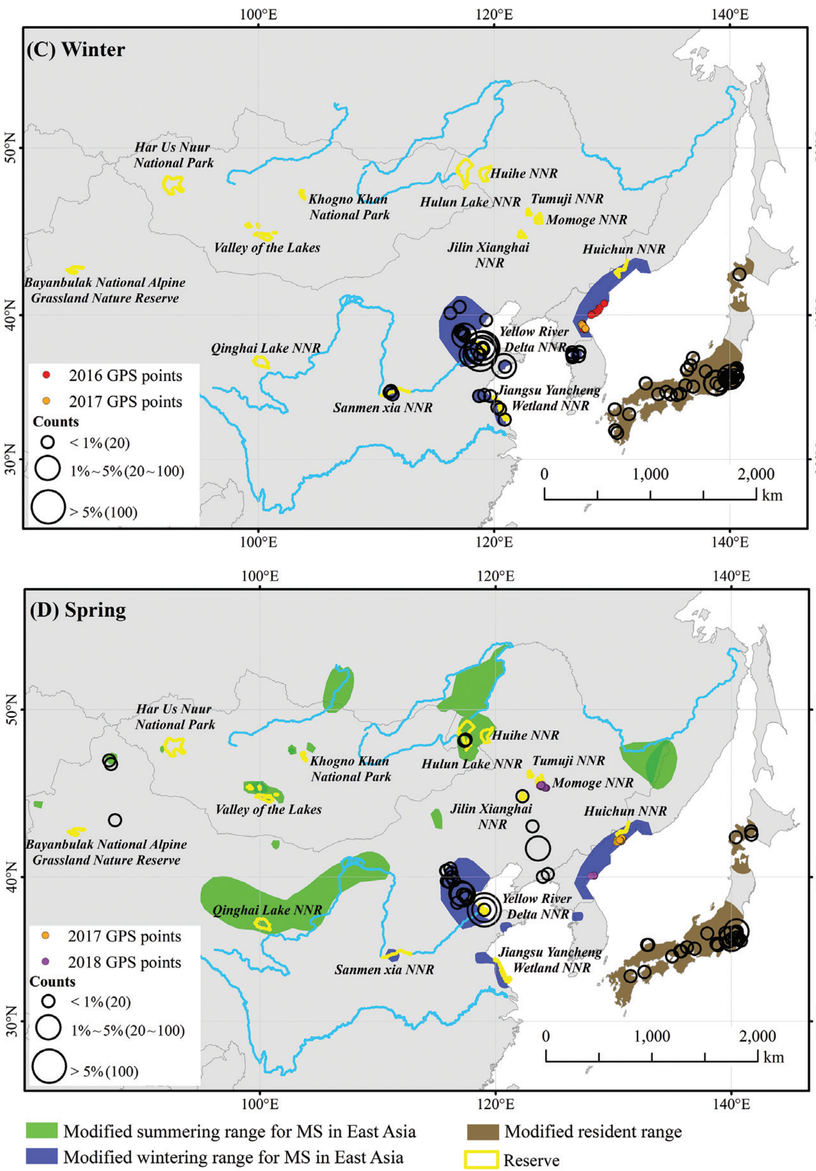

Figure 3 (continued).

stopover site, Yueliang Lake near Baicheng City, Jilin Province, China (Fig. 6). Migration distances were 2,002 km covered within 41 days in spring 2017, and 2,454 km within 34 days in spring 2018. Swans MS003 and MS004 were resighted in the wintering range of MS001 in early November, *c.* two weeks before the tracked MS001 arrived

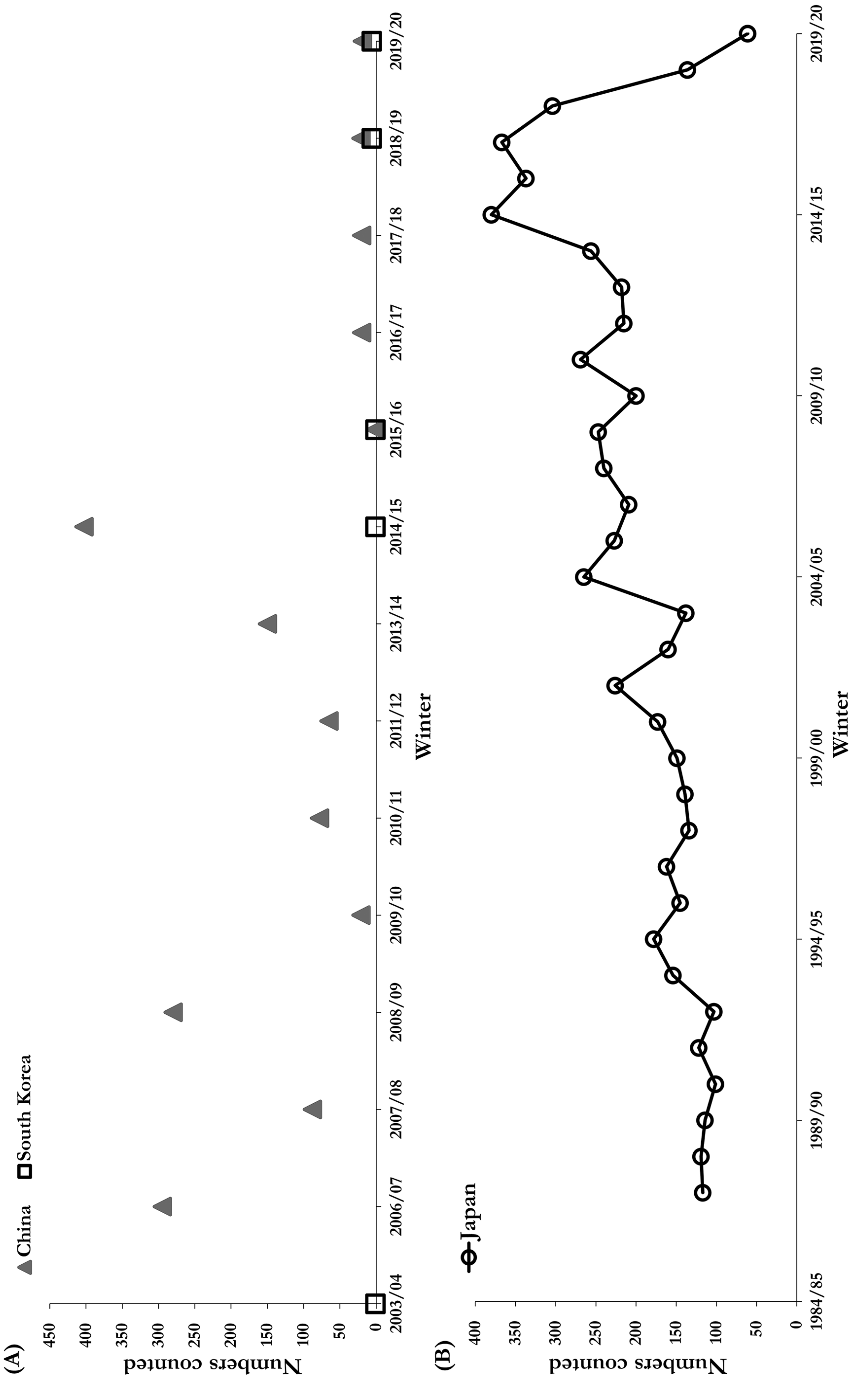

Figure 4. Total numbers of Mute Swans counted in: (A) China and South Korea in winters 2003/04–2019/20, and (B) in Japan in winters from 1987/88 to 2019/20 (Ministry of the Environment of the Government of Japan 2019; Supporting Materials Table S3).

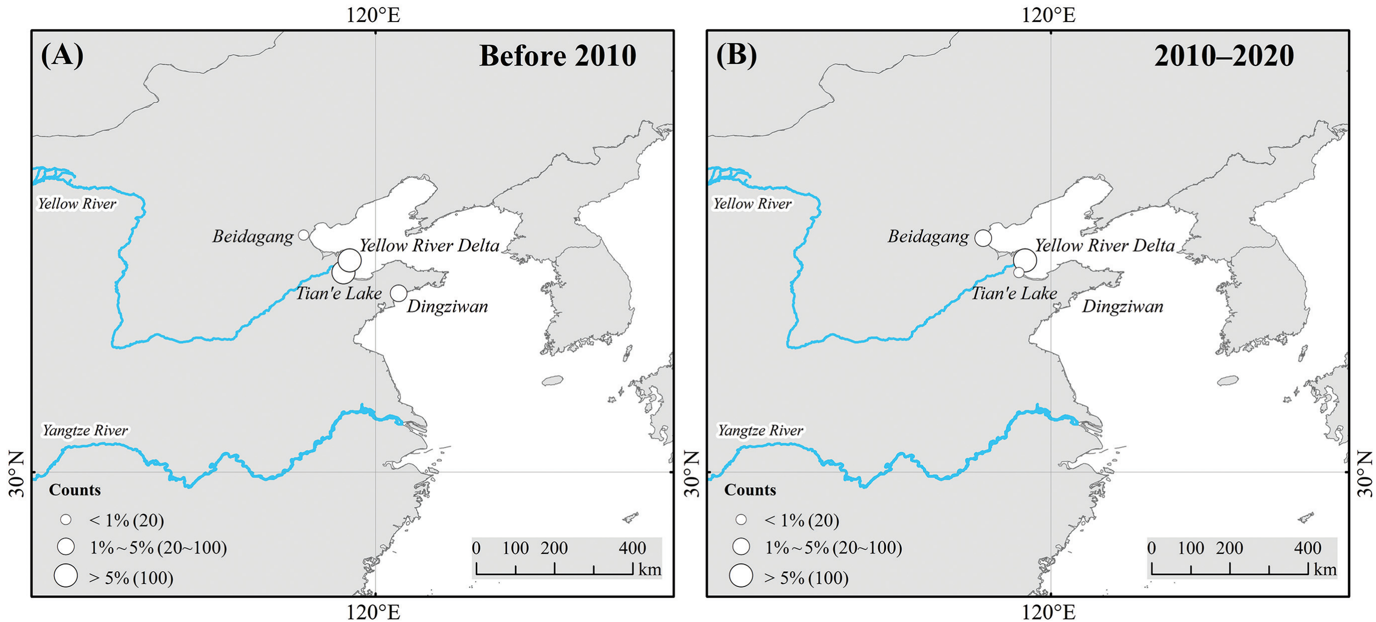

Figure 5. Map of the changes in the numbers and distribution of key wintering sites for the Mute Swan in China, based on raw counts since 2000 from eBird (Cornell Lab of Ornithology 2020) and compiled field counts by the authors and from the literature (Supporting Materials Table S2). Three key wintering sites (one 1% key sites and two 5% key sites) among four survey sites were identified before 2010 (A). Two key wintering sites (one 1% key site and one 5% key site) among three survey sites were identified during 2010–2020 (B). Count data for Dingziwan are lacking in recent years. The 1% (20 birds) and 5% (100 birds) criteria are based on the population estimates in East Asia (BirdLife International and Handbook of the Birds of the World 2019).

Table 1. Migration parameters in autumn and spring 2016–2018, for the Mute Swan tagged MS001.

Migration	Departure date	Arrival date	Migration distance (km)	Migration duration (days)	Total travel time (days)	Stopover duration (days)	No. of stopovers	Migration speed (km/d)	Travel speed (km/d)	Step length (km)	Straightness index	Flight leg
Spring	27/02/2017	10/04/2017	2,002	41.5	8.0	33.5	2	48.3	251.6	535.8	0.6	3
	10/03/2018	13/04/2018	2,454	33.9	8.4	25.5	3	72.4	291.6	501.7	0.5	4
Autumn	27/10/2016	28/11/2016	1,735	31.8	2.6	29.2	1	54.5	660.7	820.2	0.7	2
	20/10/2017	19/11/2017	2,105	30.3	2.5	27.8	1	69.5	842.1	820.7	0.6	2

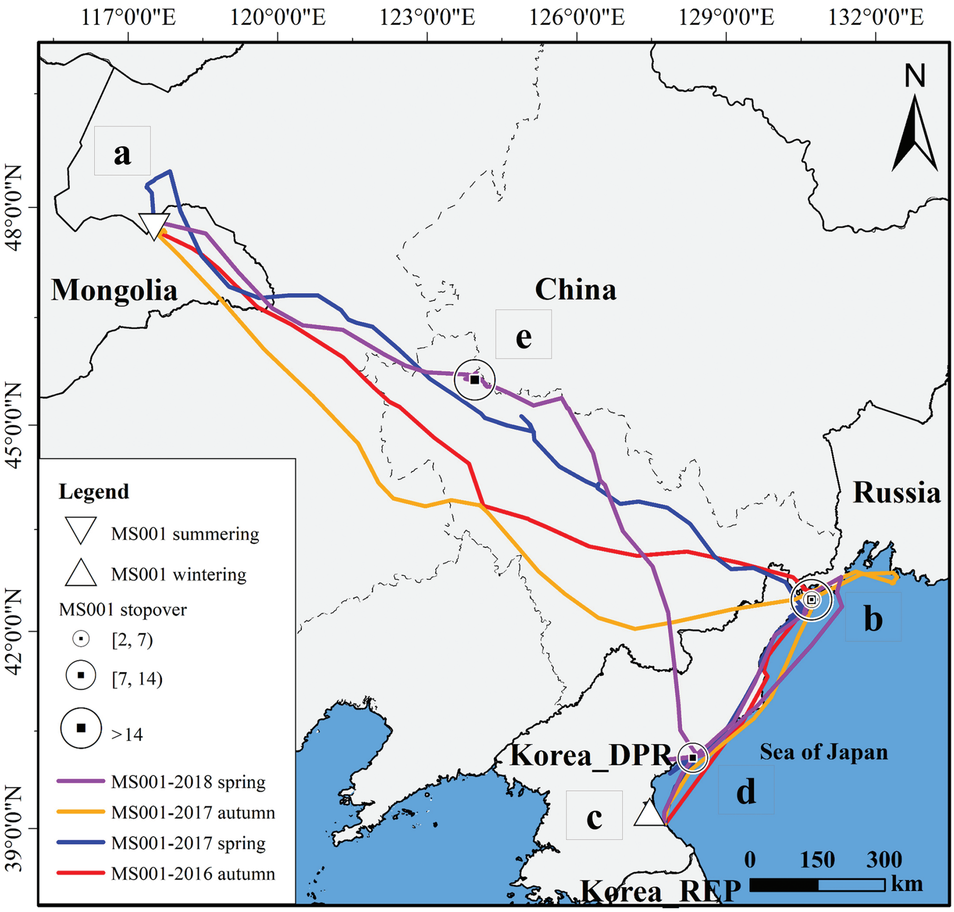

Figure 6. Spring and autumn migration routes of the Mute Swan MS001 between summering (a, Dalai Lake National Nature Reserve, China), wintering (c, the North Korean coast of the Sea of Japan) and three stopover sites (b, junction of Russia and North Korea; d, Sinpo, North Korea; e, Baicheng city, Jilin Province, China) in 2016–2018. White inverted and regular triangles = summering and wintering sites of tracked individuals, respectively. Transparent circles with solid black dots = stopover sites. Solid lines of different colours = migration routes in spring and autumn in different years.

(Fig. 2, Supporting Materials Table S1). MS002 and MS005 migrated to Inner Mongolia where the signals from their loggers terminated at stopover sites: one reached Daihai (determined from the tracking data) and the other Ulansu Lake (where the bird was resighted; Fig. 2).

Site use and movements during the annual cycle

In both tracking years, swan MS001 generally used the same summering, wintering and stopover areas (Fig. 6, Table 2). Overall, it was recorded at 11 sites (2 in summer, 2 in winter, 2 in autumn and

Table 2. Duration of stay, home range (km^2) and movements at summering, wintering and stopover sites for the tagged Mute Swan (MS001) from 2016 to 2018. Time (days) in the summering and wintering areas amounted to > two-thirds of the annual cycle; *e.g.* 286 days (78% of the year) in winter 2016/17 to summer 2017, and 303 days (83%) in summer 2017 to winter 2017/18. The home range of summering and wintering sites were larger than stopover sites. "Region" corresponds to regions labelled in Fig. 6; * = bird caught during this summer (*i.e.* data do not cover a complete summer season); UD = utilisation distribution.

Year	Period	Start date	End date	No. of fixes	Duration (days)	50% UD area (km^2)	90% UD[1] area (km^2)	Region	Centroid longitude	Centroid latitude	Daily movement (mean ± s.d. km/day)	Movement in daytime (mean ± s.d. km/hour)	Movement in night-time (mean ± s.d. km/hour)
2016	Summer*	27/09/2016 (capture date)	27/10/2016	531	30	356	1,582	a	117.53	48.36	8.70 ± 16.31	0.51 ± 2.26	0.16 ± 0.35
	1st autumn stopover	28/10/2016	26/11/2016	449	29	9	37	b	130.71	42.49	4.31 ± 5.20	0.37 ± 1.22	0.08 ± 0.22
	Winter	28/11/2016	27/02/2017	1,729	91	2,535	10,066	c	127.75	39.39	13.33 ± 27.19	1.75 ± 25.70	0.22 ± 0.50
2017	1st spring stopover	28/02/2017	10/03/2017	142	10	18	64	d	128.35	40.11	12.43 ± 28.23	0.19 ± 0.23	1.85 ± 7.43
	2nd spring stopover	11/03/2017	03/04/2017	505	23	127	413	b	130.71	42.42	13.16 ± 17.63	0.82 ± 2.77	0.20 ± 0.33
	Summer	10/04/2017	20/10/2017	4,365	193	866	4,883	a	117.59	47.71	13.22 ± 17.14	0.62 ± 2.52	0.46 ± 1.99
	1st autumn stopover	22/10/2017	18/11/2017	599	27	21	79	b	130.75	42.53	9.57 ± 7.65	0.62 ± 1.75	0.19 ± 0.36
	Winter	20/11/2017	10/03/2018	2,189	110	73	303	c	127.74	39.11	6.60 ± 9.19	0.40 ± 1.86	0.18 ± 0.37
2018	1st spring stopover	13/03/2018	15/03/2018	50	2	11	42	b	130.6	42.29	18.51 ± 12.90	1.06 ± 1.99	0.28 ± 0.19
	2nd spring stopover	15/03/2018	24/03/2018	178	9	2	13	d	128.31	40.09	8.81 ± 12.23	0.21 ± 0.37	0.67 ± 2.72
	3rd spring stopover	28/03/2018	12/04/2018	322	15	154	522	e	123.97	45.63	15.57 ± 15.59	0.72 ± 1.55	0.42 ± 1.37

5 in spring) within five areas. The summer sites were at Wulan Nuo'er in eastern Inner Mongolia in China and Buir Lake in eastern Mongolia. The distance between the centroid locations of these two summering sites in 2016 and 2017 was 72.50 km. The wintering area was at Yonghung Bay, near Wonsan in North Korea, and the distance between the centroid locations of the two wintering sites used within the bay in 2016 and 2017 was 31.2 km. Three main areas were used as staging sites during spring and autumn migration: the Ptich'ye Lake–Tongbon-p'o Lake area on the border between Russia and North Korea, Yongyeon Lake in North Korea, and Yueliang Lake in China. The Ptich'ye Lake–Tongbon-p'o Lake area was used as two spring and two autumn stopover sites, with a maximum distance of 29.4 km between them; Yongyeon Lake was used in two springs, and the distance between areas used on the lake in these years was 4.07 km; and Yueliang Lake was used as a stopover site in spring 2018.

Both the 50% UD and 90% UD of sites varied between years and across regions (Fig. 6, Table 2), with generally larger areas used at the sites visited in winter and summer than at the stopover sites.

Habitat use by swan MS001 at summer sites was similar between the two years, but differed from that at the stopover/wintering sites (Table 3). During the summer, it frequented water bodies (81.2% and 82.8% in 2016 and 2017, respectively), followed by wetlands (12.2%) and grasslands (4.9%) in 2016, or bare ground (8.0%) and wetlands (6.3%) in 2017. Elsewhere, habitat use at most stopover sites and at both wintering sites was similar, regardless of the sites or year, but was different from summering sites. At these sites, MS001 again mainly used water bodies (> 90%). At the first spring stopover site in 2017, however, the bird used mostly grassland (45.8%) and water bodies (45.1%), which conspicuously differed from its habits at other stopover or wintering sites. However, we are hesitant to draw any conclusions from data from a single individual and therefore do not test statistically for differences between seasons.

Discussion

Distribution and key sites

In this paper, satellite tracking data, survey data and expert knowledge were integrated to revise the summering and wintering range of Mute Swan in East Asia (Fig. 1). In particular, the telemetry data enabled us to extend the wintering range of Mute Swan to the northeast coast of North Korea and information from count data has extended the wintering area to include the Bohai Bay and Jiangsu coast in China. BirdLife International and Handbook of the Birds of the World (2019) show the Mute Swan to be resident in the lower reaches of the Selenga River and Amur Region in Russia, and in Inner Mongolia in China. However, our results showed that these areas are currently only used as summering and/or stopover areas. Since these areas are north of the January 0°C isotherm (Cao *et al.* 2008), open water would be frozen in winter, hence it seems unlikely that these areas are suitable as wintering habitat for the swans. The summering range of the Mute Swan has also been extended to Mongolia and Inner Mongolia as supported by multiple observations.

Table 3. Habitat use by Mute Swan tagged MS001, based on GPS locations at the summering, wintering, and stopover sites in 2016 to 2018. The main habitat used (usually water body) is indicated in bold font. "Region" labels correspond to those for the regions illustrated in Fig. 6. Habitat use in summer 2018 is not presented because of limited sample size.

Year	Period	Region	N total fixes	Cropland (%)	Grassland (%)	Wetland (%)	Water body (%)	Artificial surfaces (%)	Bare ground (%)	Forest (%)
2016	Summering	a	531	0.38	4.90	12.24	**81.17**	0.75	0.56	0.00
	1st autumn stopover	b	449	0.00	0.00	0.00	**99.55**	0.00	0.00	0.45
	Wintering	c	1,729	1.50	3.07	0.00	**91.09**	2.72	0.00	1.62
2017	1st spring stopover	d	142	4.23	**45.77**	1.41	45.07	0.00	0.00	3.52
	2nd spring stopover	b	505	0.40	0.00	0.00	**98.61**	0.79	0.00	0.20
	Summering	a	4,365	0.53	1.83	6.25	**82.75**	0.66	7.97	0.00
	1st autumn stopover	b	599	0.00	0.00	0.00	**99.67**	0.00	0.00	0.33
	Wintering	c	2,189	0.00	0.05	0.00	**99.73**	0.18	0.00	0.05
2018	1st spring stopover	b	50	0.00	0.00	0.00	**100.00**	0.00	0.00	0.00
	2nd spring stopover	d	178	1.69	0.56	0.00	**96.63**	0.56	0.00	0.56
	3rd spring stopover	e	322	4.97	1.55	0.00	**92.55**	0.93	0.00	0.00

Our compiled dataset also showed a clear seasonal distribution shift, from Mongolia and Inner Mongolia, China in summer, to the Bohai Bay and Jiangsu coast in winter. The spring and autumn distributions lay intermediate between wintering and summer. The cumulative seasonal distributional changes imply the migration routes taken by these birds, which was confirmed by the limited tracking and resighting data. One feature we failed to explain was the presence of Mute Swans in Xinjiang, China in spring, summer and autumn. The distance from this breeding distribution to the nearest known wintering areas, in Bohai Bay (*c.* 3,300 km) and Jiangsu coast (*c.* 3,600 km), are too far to suggest such a linkage, so the wintering areas of the Xinjiang breeders remains unknown and their numbers are unlikely to be included in the national mid-winter totals presented here. In addition, numbers of "resident" swans counted in Japan in summer are apparently fewer than those counted in other seasons. While this could be because sub-adult non-breeders undertake moult migration or become less accessible at the count sites, another explanation could be that some of the Mute Swans wintering in Japan migrate elsewhere to breed. In the future, we urge further tracking studies, synchronous surveys and more birdwatching data, which will help to fill these knowledge gaps of the distribution and migration range.

Abundance estimates and trends of migratory population

In the early 1990s, surveys revealed only eight wintering Mute Swans in all of China, although there is no doubt that count coverage was not exhaustive during those times. Since then the coverage of the coastal areas that are likely to hold Mute Swans has also been sporadic and non-systematic. We do know that from 1996 to 2017, numbers of Mute Swans counted on Wulansu Lake in summer rapidly increased from just four birds in 1996 to peak at 1,300 birds in 2004, although since that time numbers have fallen back to 630 in 2006, 411 in 2014 and 199 in 2017 (Zhao *et al.* 2019). We have little idea of where these birds spend the winter, but clearly they must also be added to China totals. Nineteen Mute Swans were counted during an unsystematic survey of key sites along the Yellow River estuary in January 2019, but this is likely to represent a relatively small proportion of the true numbers present. We are therefore unable to come with any realistic estimate of numbers of Mute Swans wintering in China at the present time, but suggest that it would be expedient to assume that numbers extend to at least 400 individuals, although we cannot be confident of the trends in numbers given the dearth of counts in recent decades. We also suspect that, because count coverage of Mute Swan sites in Japan may not truly reflect its winter abundance, that the recent average of 240 birds represents a conservative estimate of the total numbers nationally. Finally, although very few are detected in mid-winter waterbird counts in South Korea, we now know that some birds do likely winter along the coast of North Korea and possibly in neighbouring Russia, implying unknown wintering Mute Swan numbers there as well as at wintering sites in South Korea not covered by mid-winter counts. We therefore conclude that we are unable to make an adequate assessment of the size of the Far East Asian Mute Swan population, but consider it is more likely to be of the order of 1,000 birds than the previous estimate of 1,000–3,000, while fully acknowledging we need to improve substantially our knowledge of the species in this part of its range.

Migration routes

Movements of the bird fitted with a GPS logger enabled us to find two previously unknown wintering areas among the many potential sites that could be used by the East Asian Mute Swan population in North Korea, which summers in the Dauria International Nature Reserve, some 1,500 km away. However, it is impossible to conclude much from multiple observations of a single bird, and we should be prudent in interpreting the results derived from the tracking data in this study.

Our tracked bird mainly used water bodies throughout the year (after the first spring stopover site in 2017, when it resorted mainly to grassland, Table 3), which is perhaps not surprising, as this is in keeping with the habitat used by Mute Swans in other parts of their native and invasive ranges (Rees *et al.* 1997; Holm 2002; Wood *et al.* 2013; Zaynagutdinova *et al.* 2019; Gayet *et al.* 2020; Gehring *et al.* 2020). In a survey of three species of swans in the UK and Ireland during the winter of 1990/91, Whooper Swans *Cygnus cygnus* and Mute Swans mainly exploited shallow aquatic habitats such as lakes and rivers (68% and 61%), whereas Bewick's Swans *Cygnus columbianus bewickii* spent most time on cropland (60%). Shallow aquatic habitats and cropland are the most important foraging areas for migratory birds, and their distribution changes mainly occur in the latter (Rees *et al.* 1997).

Similar to the results from tracked Whooper Swan individuals, our single tracked Mute Swan showed within- and between-winter site fidelity. Whilst the Mute Swan mostly used water bodies during its annual cycle, however, Whooper Swans showed more seasonal variation in their use of habitat types (Ao *et al.* 2020). The migration route and wintering location of individual MS001 (Fig. 6) were located to the northeast of areas used by the East Asian Whooper Swan population (Ao *et al.* 2020; Newman *et al.* 2009). The Mute Swan made only a few, prolonged stopovers during its relatively short migration, while the Bewick's Swans tracked from Japan, had more stopovers (Chen *et al.* 2016; Fang *et al.* 2020). Both Bewick's and Whooper Swans made fewer stopovers on autumn migration than they did in the spring, which was consistent with our results for the Mute Swan (Ao *et al.* 2020; Chen *et al.* 2016).

Conservation recommendations

Despite considerable advances in our knowledge presented here, it is evident that we still know very little about the distribution, abundance and habitat use of migratory Mute Swans in East Asia. Although there remain some questions about its introduced or native status in Far East Asia, the species has been somewhat neglected and, because it is more of a coastal species in China (being exceptionally rare in the Yangtze River Floodplain, where waterbirds are now regularly counted), it has dropped through the monitoring programmes that are so effective in documenting the annual abundance of other waterbird species there. While the population remains relatively rare and dispersed, but apparently site loyal (as elsewhere throughout its global range), there is an urgent need to locate regular staging and wintering areas and establish survey mechanisms to monitor its abundance and distribution. Clearly, while we remain so ignorant about the relationships between breeding, staging and wintering sites, further telemetry studies of the species would also help in this area. In the future, it is necessary to continue and grow the existing collaboration between researchers in Russia, Mongolia, China, South Korea, and Japan and other East Asian countries to establish a long-term scientific monitoring system that is more effective at tracking changes in annual abundance and estimating the total numbers present in each country. This is especially the case in North Korea, where we now know substantial numbers likely spend the winter, and where it would be helpful to understand the potential threats to their well-being and that of the habitats upon which they depend. Climate change and continued wetland degradation, among other threats will contribute to the continued loss of wetland functions; in addition, overgrazing, development and habitat destruction will continue to reduce the extent and quality of habitat available to Mute Swans in the region. In the light of this, future research also needs to concentrate on the study of critical areas and the types of habitat used by Mute Swans throughout their annual cycle, using satellite telemetry and remote-sensing technology to provide a more scientific basis for the development of protected areas and sympathetic site management. Hopefully such collaborative research will provide the basis for assessing a full set of key sites for protection for the species, now and in the future.

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Appendix 1. Six experts from three countries discussed the distribution and migration of the Mute Swan in East Asia.

Name	Nationality	Institute
Tseveenmyadag Natsagdorj	Mongolia	Wildlife Science and Conservation Center of Mongolia
Gerelt Zhao	China	Inner Mongolia Normal University
Stephen Millington	United Kingdom	International Crane Foundation
Lei Cao	China	Research Centre for Eco-Environmental Science, Chinese Academy of Science
Xin Wang	China	Research Centre for Eco-Environmental Science, Chinese Academy of Science
Qingshan Zhao	China	Research Centre for Eco-Environmental Science, Chinese Academy of Science