Two distinct flyways with different population trends of Bewick's Swan *Cygnus columbianus bewickii* in East Asia

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Abstract

Two of the most fundamental ecological questions about any species relate to where they occur and in what abundance. Here, we combine GPS telemetry data, survey data and expert knowledge for the first time to define two distinct flyways (the East Asian Continental and West Pacific flyways), migration routes and abundance for the Eastern population of Bewick's Swan *Cygnus columbianus bewickii*. The Eastern population is the largest flyway population, supporting *c.* 77% of Bewick's Swan numbers globally. GPS telemetry data showed that birds breeding in the Russian arctic from the Yamal Peninsula to *c.* 140°E (including the Lena and Yana Deltas), winter in the middle and lower reaches of the Yangtze River in China (which we label the "East Asian Continental flyway"). Bewick's Swans breeding from the Indigirka River east to the Koluchin Bay winter in Japan, mostly in Niigata, Yamagata and Ishikawa Prefectures (the "West Pacific flyway"). There was no overlap in migration routes used by tagged individuals from the two flyways. Counts of Bewick's Swans in the East Asian Continental flyway during the 21st century have shown wide between-year variations, reflecting incomplete coverage in earlier years. Bewick's Swans in this flyway currently numbers *c.* 65,000 birds based on extensive wintering survey coverage, compared to *c.* 81,000 in the early 2000s, based on less complete coverage. Chinese-wintering swans now concentrate mainly (*c.* 80%) at Poyang Lake in Jiangxi Province and Hubei Lakes (mostly in Longgan Lake), compared to a more widespread distribution both within Poyang and throughout the Auhui Lakes in 2004 and 2005. In contrast, Bewick's Swans of the West Pacific flyway now numbers *c.* 40,000, compared to just 542 in 1970. This population has shown no significant overall change since 2004, when it numbered *c.* 45,000 birds. Small numbers within this population probably also winter in South Korea. These results provide our first basic understanding of the winter distribution of Chinese- and Japanese-wintering Bewick's Swans in relation to their breeding areas, confirming the need to coordinate future research and monitoring in the two flyways, as well as the need for more information on swans wintering in South Korea.

Key words: Bewick's Swan, *Cygnus columbianus bewickii*, distribution range, migration routes, population size, population trends, winter abundance.

Bewick's Swans *Cygnus columbianus bewickii* breed across the open maritime tundra of the Russian arctic and migrate to discrete wintering areas ranging from northwestern Europe to East Asia (Rees 2006; BirdLife International and Handbook of Birds of the World 2019). The global population size of this subspecies was estimated at *c.* 120,000 in 2015 (Rees *et al.* 2019), and three main populations were identified based on their winter distribution and migration routes: the Northwest European, the Caspian (currently the subject of re-analysis) and the Eastern populations (Rees & Beekman 2010).

It is relatively well established that Bewick's Swans wintering in northwest Europe – mainly in the UK and the Netherlands, but increasingly in Germany (Augst *et al.* 2019; Beekman *et al.* 2019; Nuijten *et al.* 2020), and also extending to southernmost France – migrate to breed in European arctic Russia, west of the Ural Mountains (Rees 2006; Nuijten *et al.* 2014; Griffin *et al.* 2016). Following a 39% decline in numbers from 29,780 to 18,057 birds between 1995 and 2010, this population is considered as Vulnerable (BirdLife International 2004), though there is some recent evidence that the decline may have plateaued with a slight recovery to *c.* 20,150 birds counted during the 2015 international swan census (Beekman *et al.* 2019). Data concerning Bewick's Swans wintering around the Caspian Sea area are extremely scarce. There, numbers are thought to have increased from 500–1,000 birds in the late 20th century to *c.* 800–3,000 during 2011–2015 (Wetlands International 2019). Previously virtually unknown in the southeastern Balkans, Bewick's Swans were first observed regularly wintering in Greece during the late 1990s (D. Vangeluwe, unpubl. data), where numbers increased to *c.* 10,000 individuals by 2017. The relationship between these birds and the Caspian population of the species is unclear and currently the subject of study. Recent satellite tracking and ringing studies (Vangeluwe *et al.* 2018) have shown that swans from both wintering areas are sympatric at their breeding grounds on the Yamal Peninsula.

The Eastern population of Bewick's Swans, the largest among the three currently recognised populations on the Eurasian continent, has recently been found to breed from Yamal Peninsula eastwards (Vangeluwe *et al.* 2018). The breeding range extends to Koluchin Bay (Kistchinski 1988; Higuchi *et al.* 1991; Rees 2006), where they overlap with the Nearctic subspecies Whistling Swans *Cygnus columbianus columbianus* in northern Chukotka Peninsula (Arkhipov *et al.* 2013). This population is thought to number *c.* 90,000 birds, with fluctuating population trends (Rees *et al.* 2019), most of which winter in China and Japan, with very few individuals occurring in South Korea (Jia *et al.* 2016).

The largest numbers of Bewick's Swans wintering in East Asia occur in China, but the absence of extensive coordinated national counts makes it impossible to determine trends in abundance for China between 1970 and the early 2000s. Wintering numbers counted in China fluctuated between winters during 2003/04–2010/11, probably due to uneven count coverage between years. Elsewhere, systematic count programmes found that numbers wintering in South Korea declined from 792 in winter 1998/99 to 72 in 2010/11, while birds wintering in Japan increased from 31,198 in 1995/96 to 36,810 in 2010/11 (Jia *et al.* 2016). Whether such changes in abundance are attributable to a shift in winter distribution between the three countries, or reflect population changes on the wintering, staging or breeding areas, is impossible to determine without investigating the connectivity of individuals in the Eastern population and links between sites along the flyways of these subpopulations. In order to understand the reasons for differences in the population trajectories of different subpopulations, and thus ensure appropriate management actions, it is essential to be aware of the migratory connectivity between their breeding and wintering sites, and the potential dispersal of birds within the wintering range.

The rapid development and application of tracking technology has provided valuable information on Bewick's Swan migration routes across Asia in recent years. The first tracking study revealed that one of four Bewick's Swans caught on Hokkaido, Japan, in 1990 migrated successfully to breed near the Kolyma River in Russia (Higuchi *et al.* 1991). A subsequent study followed 16 Bewick's Swans, also caught on Hokkaido during 2009–2012, which migrated through Sakhalin Island, the Kamchatka Peninsula and the Kolyma River, to breed in tundra areas between the Alazeya and Chaun Rivers (Chen *et al.* 2016). This migration route between eastern arctic Russia and Japan was also used by 10 birds caught in the Chaun Delta in summer 2016 (Wang *et al.* 2018). In contrast, two Bewick's Swans caught at Dongting Lake in the Yangtze River floodplain, China, during winter 2016/17 migrated to spend the summer on the Yamal Peninsula and at Yana Bay, respectively (Huang *et al.* 2018). Six of the 11 birds caught on the Yamal Peninsula during the summers of 2015–2017, migrated along the Ob River, and through the Basin of Great Lakes in Mongolia, to winter mainly at Poyang Lake in China (Vangeluwe *et al.* 2018). While these studies provided some evidence to argue for the existence of a flyway structure for the Eastern Bewick's Swan population, the sample sizes and geographical distribution were insufficient, especially among birds wintering in China, to confirm boundaries between discrete flyways within East Asia.

In this study, we augment the earlier telemetry studies by tracking a further 140 marked individuals from a range of sites, to describe their summering, staging and wintering areas, with a view to confirming migratory flyways for Bewick's Swans wintering in East Asia. Additionally, we integrate the new telemetry data with results of wintering waterbird surveys and expert knowledge, to provide a better assessment of the population trends for Bewick's Swans wintering in the region. Overall, we aim to identify biologically meaningful flyways, update information on the swans' conservation status, and thereby improve the basis for the effective management of the largest Bewick's Swan population in Eurasia.

Methods

Migration data

We combined tracking data and banding data from Bewick's Swans in East Asia with experts' knowledge of waterbird movements and distribution (compiled during a symposium held in Beijing in October 2019; Appendix 1) and a review of the Bewick's Swan literature, to delineate ranges and flyways for Bewick's Swans in the region. Moulting swans and growing cygnets were caught when flightless in summer by capturing individual birds from a boat. On the winter quarters, full-grown individuals were caught at night by dazzling them with powerful lamps; on the staging area, swans were captured using net traps or by hand. The extent of grey juvenile feathering was used to determine the age of the swans (Rees 2006) and the sex of each bird was determined by cloacal examination or genetic determination. A total of 238 Bewick's Swans were caught and tagged with GPS transmitters in East Asia during 2014–2018, including 211 birds at four key sites across the breeding range, nine birds at three key staging sites and 18 birds at two key wintering sites (Table 1). Of these, location data recorded for 140 individuals with at least one complete spring or autumn migration were used to identify the flyway corridors (Table 2).

The 140 birds which provided tracking data used to describe migration corridors included 133 yearling or adult Bewick's Swans caught and fitted with GPS transmitters at four moulting areas in different parts of the Russian arctic during summers 2015–2018 inclusive: 13 on the Yamal Peninsula (68°15'N, 68°11'E) in 2015–2017; 19 in the Lena River delta (72°46'N, 127°28'E) in 2017; six in the Indigirka Delta (70°45'N, 151°28'E) in 2018; and 95 in the Chaun River delta (68°53'N, 170°58'E) in 2016–2018. Three more swans were tracked from their staging areas: one at Uws Lake, Mongolia (50°27'N, 93°14'E) in August 2017; one at Hui River, China (48°57'N, 119°39'E) in April 2018 and one at Lake Kutcharo, Japan (45°7'N, 142°20'E) in April 2017. Four Bewick's Swans were caught at two sites on the main wintering grounds along the Yangtze River floodplain, China: one at Poyang Lake (29°07'N, 116°16'E) and three at

Table 1. Summary data for 238 Eastern population Bewick's Swans caught and fitted with solar-powered GPS/GSM telemetry devices during 2014–2018: 211 at four key sites across the breeding range, nine at three key staging sites and 18 at two key wintering sites.

Capture sites		**Coordinate**		**Capture period**	**Age**				**Sex**			**Total**
		Latitude	**Longitude**		**Adult**	**Subadult**	**Juvenile**	**Unknown**	**Female**	**Male**	**Unknown**	
Breeding area	Yamal Peninsula	68.250	68.183	2015–2018	13	19*	0	0	16	16	0	32
(n = 211)	Lena River delta	72.767	127.467	2017	20	0	0	5	16	9	0	25
	Indigirka River delta	70.750	151.467	2018	7	0	0	0	0	0	7	7
	Chaun River delta	68.883	170.967	2016–2018	121	3	23	0	31	31	85	147
Staging sites	Uws Lake	50.450	93.233	2017	0	1	0	1	2	0	0	2
(n = 9)	Hui River	48.950	119.650	2018	0	0	0	1	0	0	1	1
	Lake Kutcharo	45.116	142.333	2017	6	0	0	0	2	3	1	6
Wintering area	Poyang Lake	29.117	116.283	2016	1	0	2	0	0	0	3	3
(n = 18)	East Dongting Lake	29.216	112.800	2015	0	0	0	15	0	0	15	15

Note: * indicates birds in their 2nd summer (one year old).

Table 2. Summary of the satellite tracking data recorded for 140 Bewick's Swans that were tracked for at least one full migration during 2014–2019, which provided the basis for determining the two flyways in East Asia. A total of 48 spring and 176 autumn tracks were recorded, including 28 spring and 59 autumn tracks for 38 birds of East Asian Continental flyway, and 20 spring and 117 autumn tracks for 102 birds of West Pacific flyway.

Flyways	Capture sites	Tracking period	Individual birds	Spring tracks	Autumn tracks	Migration routes
East Asian Continental	Yamal	2015–2019	13	17	30	Yamal–China
	Lena Delta	2017–2019	19	4	23	Lena–China
	Uws Lake	2017–2018	1	1	1	Yamal–China
	Hui River	2018–2109	1		1	Lena–China
	Dongting Lake	2014–2017	3	5	4	Yamal/Yana/Hulun Lake–China
	Poyang Lake	2016	1	1		Mongolia–China
	Total	2014–2019	38	28	59	
West Pacific	Indigirka River	2018–2109	6		6	Indigirka–Japan
	Chaun Delta	2016–2109	95	20	110	Chaun/Kolyma–Japan
	Lake Kutcharo	2017–2018	1		1	Kolyma–Japan
	Total	2016–2019	102	20	117	
Overall total			140	48	176	

East Dongting Lake (29°13'N, 112°48'E) between December 2014 and March 2016.

The birds were each tagged with one of several types of solar-powered collar-mounted transmitters used in this study (Druid Technology, China, 35 g and 46 g; Ornitela, Lithuania, 55 g; Hunan Global Messenger Technology Company, China, 27 g; KoEco, Republic of Korea, 103 g; Ecotone, Poland, 35 g), which recorded GPS positions and transmitted data via the GSM mobile networks (for full details see Supporting Materials Table S1). These transmitters provided 113 ± 57 (mean ± s.d., range = 2–227) GPS positions per day, depending on the power supply and settings. First-day movement data after the birds were captured and tracked, and last-day data before birds died or we otherwise lost contact with devices, were excluded from all the analyses in case behaviour during these periods were aberrant. The GPS points between arrival and departure summering sites were identified using the method described by Wang *et al.* (2018).

Distribution and migration range

The breeding and wintering distributions of Bewick's Swans in Asia were defined in ArcGIS 10.2 (ESRI 2013), based on the maps generated by BirdLife International and Handbook of the Birds of the World (2019). This distribution map had recently been reviewed and updated by the Handbook of the Birds of the World team, using published literature and other information sources up to and including 2017. We revised these maps in line with winter survey data (see *Abundance estimates and trends* below), and information on the summer and winter distribution of individual birds described by the satellite tracking data (see *Migration data* section above), supported by expert knowledge of areas used by the swans across their range. Migratory flyways used by birds within the Eastern Bewick's Swan population were likewise determined from the ringing and tracking data, and from a literature review. All data sources were discussed during the symposium convened in October 2019, and the distribution and migration routes agreed by 10 experts from five countries in the East Asia flyway attending the meeting.

Abundance estimates and trends

As the Eastern population of Bewick's Swans winters mainly in China, South Korea and Japan, and different methods are used by each of these three countries to assess numbers of wintering waterbirds nationally, it has been expedient to divide this population into these wintering groups to monitor the number of swans wintering in East Asia.

Abundance estimates for the Chinese-wintering part of the population prior to 2012 were published in Jia *et al.* (2016). Synchronous Yangtze waterbird surveys undertaken during mid-January to early February in winters 2003/04 and 2004/05, and more recently in winters 2015/16 and 2017/18–2019/20 inclusive, are considered to cover most Bewick's Swans wintering in China (Cao *et al.* 2010; Jia *et al.* 2016). The survey methods used in 2015/16 and 2017/18–2019/20 were consistent with those used to count waterbirds wintering in the middle and lower reaches of the Yangtze River floodplain in 2003/04 and 2004/05 (Barter *et al.* 2004, 2006), except that some new survey sites were added based on satellite tracking data from Bewick's Swans in 2018/2019 and 2019/2020.

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 coordinated annual nationwide censuses at most lakes, reservoirs, lengths of seashore and bays known to be important for waterbirds during the non-breeding period since 1999. The simultaneous two-day field counts, made in mid- or late January each year, are undertaken by ornithologists, experienced birdwatchers and volunteers to estimate the distribution and abundance of wintering waterbirds in South Korea.

In Japan, the "Annual Census of Waterfowl (Anatidae) Population" has been conducted by the Ministry of the Environment, with the assistance of prefectural governments, on *c.* 15 January since 1970. This nationwide survey covers all main wintering sites for swan, goose and duck species throughout the country during the non-breeding season (Ministry of the Environment Government of Japan 2019).

Bewick's Swans from the East Asian region are not known to winter regularly in any other countries, with small numbers reported from South Korea (Cao *et al.* 2008) and occurring only as vagrants elsewhere. We therefore consider that coverage of these three nations is effective for assessing the numbers of birds in the region as a whole.

Due to incomplete coverage of the winter surveys in China prior to 2012, the size of the wintering population is estimated from counts at sites visited in the Yangtze River floodplain (Cao *et al.* 2010; Jia *et al.* 2016). Subsequent surveys were thought to cover most key areas used by Bewick's Swans wintering in China, and these data provide a fuller assessment of wintering numbers. National waterbird surveys have been carried out systematically in South Korea (since the 1990s) and Japan (since 1970), so annual counts can be used to describe total wintering numbers for these countries each year. Simple linear regressions were applied to $\log_{10}$-transformed annual count data to detect the general trends for China, South Korea and Japan. Temporal trends in counts of long-lived waterbirds may however be temporally autocorrelated (*e.g.* Wood *et al.* 2019), so initial assessments were made of linear regression residuals for the temporal trends in count data for each country, fitted using the nlme package in Program R (Pinheiro *et al.* 2020; R Core Team 2020). Inspections of the resulting autocorrelation plots showed evidence of statistically significant ($P < 0.05$) residual temporal autocorrelation in the regression models for Japan and South Korea, but not China. To assess 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). Autocorrelation structures were included in each model according to the years over which significant residual autocorrelation was detected; China = 0, South Korea = 2, and Japan = 7. 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, and is thus analogous to 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).

Key wintering sites in China and Japan

Key wintering sites in China and Japan were determined from survey data recorded during winters 2015/16–2019/20, and considered to be those that exceeded 1% of the national count totals at least once during this period.

For China, the current estimate of wintering numbers was taken as the average of the total numbers counted during surveys in winters 2018/19 and 2019/20. These data were considered the most reliable in terms of coverage, whereas for Japan and South Korea estimates were taken as the average of the maximum counts recorded each winter over the last five years: in winters 2014/15–2018/19 for Japan and 2015/16–2019/20 for South Korea.

Changes in the number and distribution of the species at key sites in China over the past 15 years were investigated by comparing annual maximum counts at these sites from 2003/04 to 2019/20, mindful of the general improvement in coverage over this period. In addition to the survey data mentioned in the *Abundance estimates and trends* section of the Methods, surveys of key sites (Poyang Lake, Dongting Lake, Hubei, and Anhui Lakes) along the Yangtze River floodplain in winters 2005/2006, 2007/2008–2014/2015 and 2016/2017 were also included.

We used data from the 2015/16–2018/19 "*Annual Census on Waterfowl* (*Anatidae*) *Population*" (Ministry of the Environment Government of Japan 2019) to identify key sites in Japan. All Anatidae species are counted at > 9,000 sites during the mid-January surveys, but survey methods vary between sites, so swans were counted at foraging sites (*e.g.* rice paddies) as well as at roosts. Kernel density, weighted by the total number of Bewick's Swans counted was estimated for each year at 5 × 5 km resolution. All cells with densities in excess of 5 swans/km^2 were extracted and the ranges were combined across years. Annual counts of Bewick's Swans in those cells were extracted, and assigned to the nearest roost sites (most of the roosts were associated with open water areas), based on expert opinion. The roost sites supporting ≥ 1% of the derived total national estimates were defined as key sites in Japan.

Results

Breeding and wintering distribution

Bewick's Swans in East Asia breed from Yamal Peninsula (68°14'N, 68°10'E) in the west across to the Koluchin Bay (67°4'N, 174°30'W) in the east, also extending to the Lyakhovskie Islands and Wrangel Island in northern Russia (Fig. 1), although breeding on Wrangel Island is considered to be irregular (Stishov 2004).

The wintering range of the Eastern Bewick's Swan population, previously

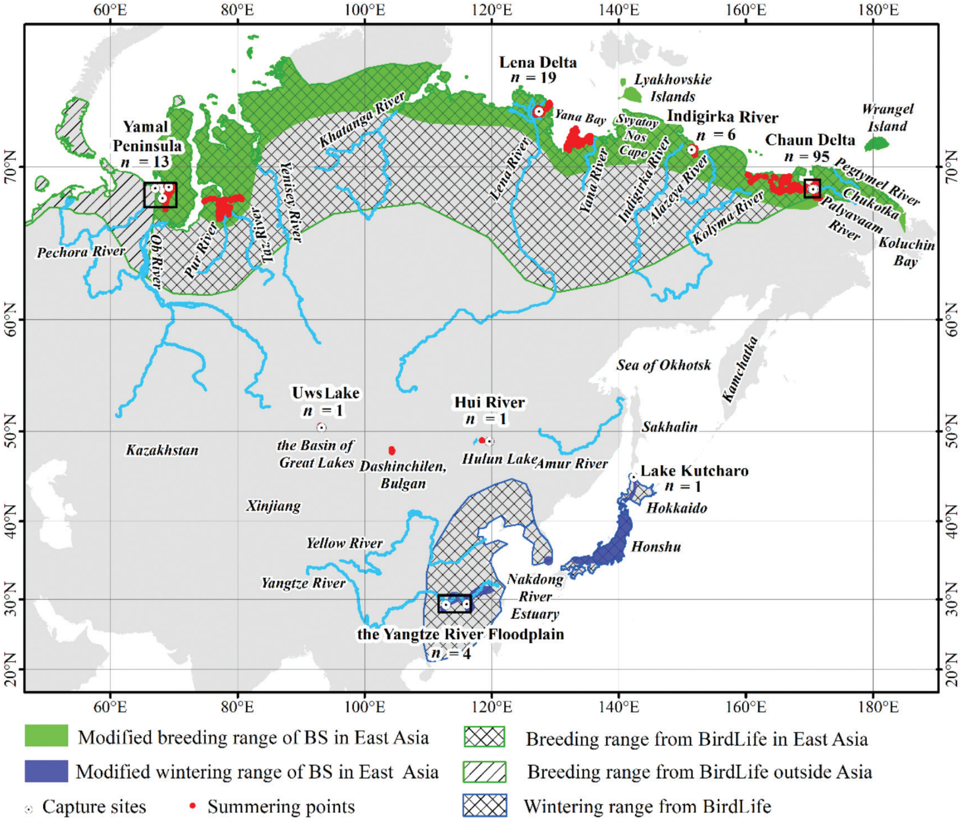

Figure 1. Revised distribution map of the Bewick's Swan in East Asia, including breeding (from Yamal Peninsula to Koluchin Bay) and wintering ranges (Yangtze River floodplain in China, Nakdong River Estuary in South Korea, Honshu Island in Japan), which are shaded in green and blue, respectively, modified from BirdLife International and Handbook of Birds of the World (2019). The revised breeding range is based on tracking data (red points denoting GPS points generated during the period between each individual point from arrival to departure at the summering grounds) and expert knowledge, and revised wintering range was based on field surveys data and expert knowledge (see *Methods* for details). One hundred and forty individuals tracked successfully were among birds caught at four key sites (the Yamal Peninsula, Lena Delta, Indigirka River and Chaun Delta) across the breeding range, at one key wintering site (Yangtze River floodplain) and three key staging sites (Uws Lake, Hui River and Lake Kutcharo) in East Asia. Circles with black dots = capture sites, n = number of birds that completed at least one spring or autumn migration (Table 2). All the site/area names mentioned in the paper are shown on the map.

defined as China, South Korea and Japan, was confirmed by the telemetry results. It was originally thought that the wintering range in China covered the middle and lower reaches of the Yangtze River floodplain (hereafter MLYFP), including Poyang Lake in Jiangxi Province and Anhui Lakes (Cao *et al.* 2010; Cong *et al.* 2011). Survey data since 2014/15 however showed that the species has changed its wintering distribution, and it is now mostly confined to Poyang Lake in Jiangxi, Longgan Lake in Hubei Province, Dongting Lake in Hunan Province and Shijiu Lake in Jiangsu Province (Fig. 2). In South Korea, total numbers of Bewick's Swans currently number < 100 birds, but they too show some contraction of range, now being largely confined to the Nakdong River Estuary (Fig. 1). Most Japanese-wintering Bewick's Swans occur in the northern and middle part of the country, mainly on Honshu Island, with very few in Hokkaido (Fig. 1).

Migration routes

Two discrete flyways for the Bewick's Swan in East Asia could be identified from 224 complete migration tracks, provided by 140 different individuals (Fig. 3). One connects the tundra of Siberia to China; the other connects the tundra of the Russian far east to Japan. We here identify these as the "East Asian Continental flyway" (comprising swans breeding in the Lena, Yana and Yamal regions, which migrated to China), and the "West Pacific flyway" (comprising swans breeding from the Indigirka River east to Koluchin Bay, which wintered in Japan). Despite the discreteness of these flyways, indicated by the flight-lines of the tagged swans, each was characterised by considerable variation in migration routes taken by individuals. The East Asian Continental flyway, which included the birds from the Yamal Peninsula and also those from Lena/Yana, followed different routes to China. Swans using the West Pacific flyway in contrast were channelled to some extent along the Kolyma River, across the Sea of Okhotsk and over Sakhalin Island to Japan.

The four swans caught in winter along MLYFP mostly migrated to breeding areas on the Yamal Peninsula and Yana Bay, although some (presumably non-breeding birds) summered in Mongolia and Inner Mongolia, which are not regular summering areas for Bewick's Swans. Birds caught on the staging areas at Uws Lake and along the Hui River migrated to breeding areas in the Lena Delta and on the Yamal Peninsula, and subsequently wintered along the MLYFP. Information relating to this flyway came from full migration data obtained from 38 individual Bewick's Swans (28 spring tracks and 59 autumn tracks; Table 2). The 13 individuals tracked from Yamal Peninsula to the MLYFP cumulatively provided data for 30 autumn and 17 spring migrations. These swans mostly migrated south along the River Ob, through the Siberian lowlands, and via Mongolia and western Inner Mongolia to wintering sites in the MLYFP. Although one bird moved further south along the River Ob valley, before moving through Kazakhstan to reach wintering grounds in Xinjiang Province. This individual migrated to the Poyang Lake area for the following two winters. The 19 individuals caught and GPS-tagged in the Lena Delta that provided full migration tracks (23 in autumn; four in spring), migrated along the Lena River, via eastern Inner Mongolia to winter in the MLYFP. A bird caught on the Hui River in Inner Mongolia, migrated to the Lena Delta for the summer and subsequently wintered in the MLYFP. One of the birds, caught in the Yangtze River floodplain, which was tracked successfully,

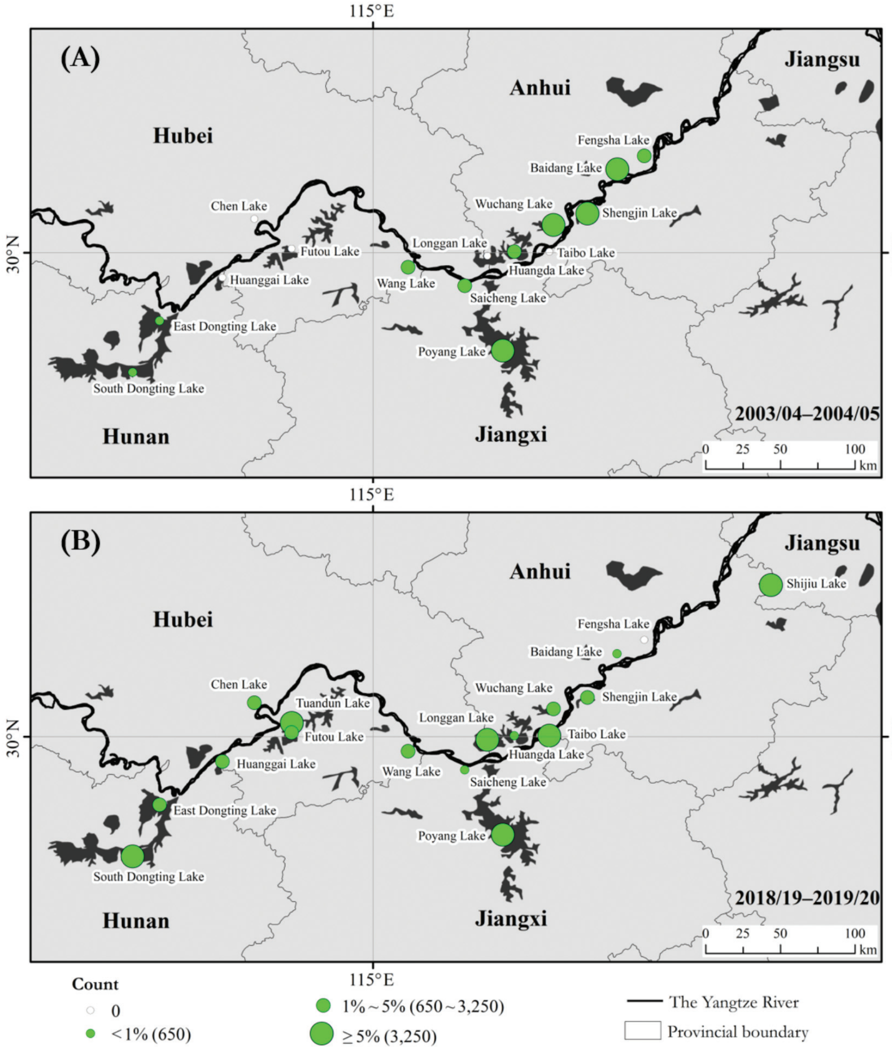

Figure 2. Changes in the numbers and distribution of key wintering sites in the Yangtze River floodplain, China, between: (A) winters 2003/04–2004/05 (15 key sites, including eight with ≥ 1% of swans counted), and (B) winters 2018/19–2019/20 (17 key sites, including 13 with ≥ 1% of swans counted). In recent years, the main wintering distribution of Bewick's Swans has spread from Jiangxi and Anhui provinces to Hubei, Hunan, and Jiangsu provinces, but the wintering numbers using Anhui Lakes declined significantly. Two lakes (Tuandun and Shijiu Lakes) were added as new survey areas during winters 2018/19 and 2019/20 because satellite tracking data indicated that these were being used by Bewick's Swans. White circles indicate sites that were visited but where no swans were present. The size of the green circles indicates the numbers counted as a proportion of individuals, in relation to the total numbers counted in China that winter.

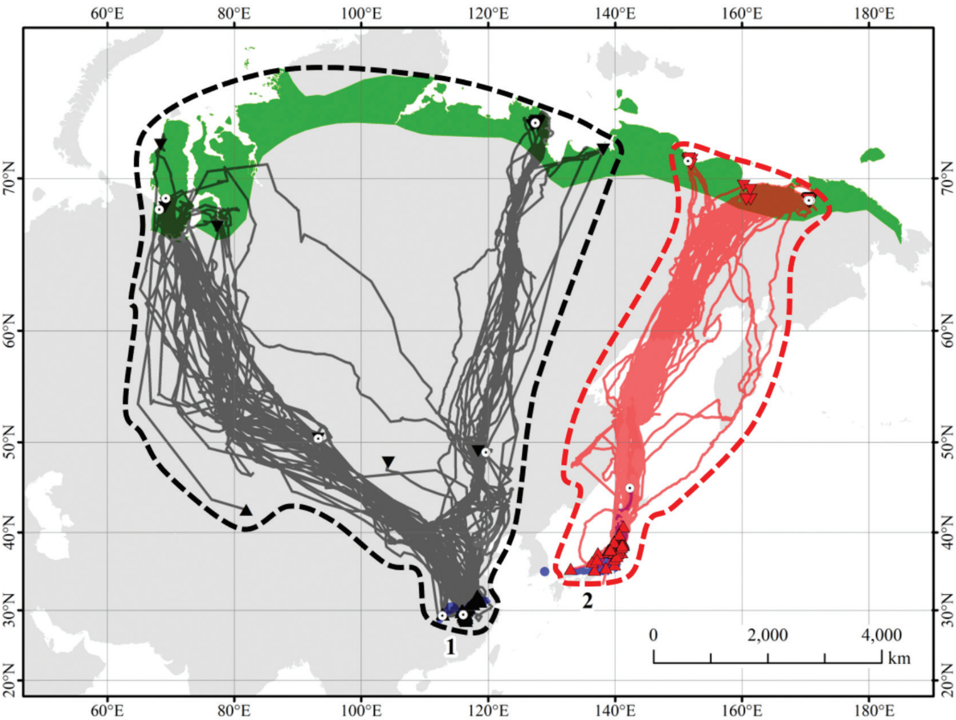

Figure 3. Two distinctive flyways described for Bewick's Swans in East Asia: (1) the East Asian Continental flyway (black dashed line; birds bred between the Yamal Peninsula and Svyatoy Nos Cape; wintered in China), and (2) the West Pacific flyway (red dashed line; swans bred between the Indigirka River and Chaun Delta; wintered in Japan). The East Asian Continental flyway was defined by the migration routes of 39 tagged individuals (black solid lines) wintering in China. These include 33 Bewick's Swans caught in the breeding range on the Yamal Peninsula (n = 14) and Lena Delta (n = 19), and two birds caught on staging sites at Uws Lake (n = 1, summered on the Yamal Peninsula) and Hui River (n = 1, summered in the Lena Delta), which all wintered in China. Additionally, of birds caught in winter on the Yangtze River floodplain (n = 4), one bred on the Yamal, one bred in Yana Bay, and two summered on the Mongolian steppe. The West Pacific flyway was defined by migration routes of 102 individuals (red solid lines) from the Japanese wintering population, including Bewick's Swans caught on breeding areas near the Indigirka River (n = 6) and on the Chaun Delta (n = 95), which migrated to Japan. In addition, a bird caught in spring at Lake Kutcharo, bred in the Kolyma River estuary and wintered in Japan. Circles with black dots = capture sites; light green shaded areas = our revised breeding range; dark blue areas = the revised wintering range. Inverted and regular triangles represent breeding/summering and wintering areas used by tracked individual(s), respectively. Population sizes and trends are from the results from this study, based on count data from China (1988–2020) and Japan (1970–2019) winter surveys.

migrated through eastern Mongolia and along the Lena River, and summered in the delta of the Yana River.

Our tracking revealed one unusual pattern of Bewick's Swan migration. Some subadult birds may summer far south of the normal breeding range, in the forest and even the steppe zones. Of two birds tracked from the wintering grounds in China, one (bs004, a juvenile) summered in Dashinchilen, Bulgan, in the northern part of Mongolia, later returning to capture locations in the MLYFP to winter, and another (bs001, unknown age) summered on a small lake near Hulun Lake, eastern Inner Mongolia. A swan (bs005, unknown age) caught on Uws Lake in northwest Mongolia during the summer, migrated that autumn through eastern Mongolia, to winter in the MLYFP, before summering on the Yamal Peninsula in the following year.

Bewick's Swans of the West Pacific flyway included birds caught on the breeding areas in the deltas of the Indigirka and Chaun Rivers, which wintered in Japan, and also birds caught at one staging area, which migrated to breeding areas along the Kolyma River and subsequently wintered in Japan. Full migration data were obtained for 102 Bewick's Swans on this flyway (20 spring tracks; 117 autumn tracks). The six birds caught near the Indigirka River and 95 individuals caught in Chaun Delta all migrated via the Kolyma River valley and Sea of Okhotsk, primarily using staging areas in Piltun Bay on Sakhalin Island or near the Amur River estuary, although a few flew via the Kamchatka Peninsula. From here, they continued to winter areas on Honshu Island, Japan. The one bird caught on Lake Kutcharo in Japan, migrated through Sakhalin Island and the Kolyma River, to summer in the Kolyma Delta. Individuals tagged at each of the catch sites passed through the same apparently critical stopover sites on the Lower Kolyma River and northern Sakhalin Island.

Population sizes and trends of wintering populations

From our contemporary counts of *c.* 65,000 in China, 40,000 in Japan and 10 in Korea, we suggest that the Eastern Bewick's Swan population in East Asia numbered *c.* 105,000 individuals in winter 2019/20. This is not a significant change compared to the 110,000 estimated during 1999/2000–2004/05 (Table 3). Wintering numbers in South Korea declined significantly from 792 birds in January 1999 to just 10 individuals in January 2020 (Table 4, Fig. 4, Supporting Materials Table S2); we therefore consider that the species is now effectively extinct in South Korea.

The *c.* 65,000 wintering in China exceed all those wintering elsewhere in East Asia, although this estimate falls short of the *c.* 81,000 counted in 2004/05 based on less complete coverage. The contemporary estimate comes from large survey efforts, which attempted to cover all the known and new key sites identified from telemetry data throughout the Yangtze (Table 3, Fig. 4). Annual survey data during 2004/05–2019/20 showed a declining trend for Bewick's Swans wintering in China, although there was no statistically significant decline detected from 1988/89 to 2019/20 (Table 4). Recognising that the survey coverage achieved in the 1990s was very

Table 3. Abundance estimates and 1% criteria for the two Bewick's Swan flyways and for the entire Eastern population of Bewick's Swans, based on wintering survey data (1999/2000–2019/20) in China, South Korea and Japan.

Timing of population estimate	East Asian Continental flyway	West Pacific flyway		Total Eastern population
	China	South Korea	Japan	
Population estimate in 2000–2005	81,000[a]	259[b]	30,350[b]	110,000[a]
Population estimate in 2007–2011[c]	80,000	56	40,000	120,000
New Population estimate in 2019–2020	65,000[d]	10[e]	40,000[f]	105,000
New 1% criteria in 2019–2020[g]	650	–	400	1,050

Notes: [a]data from Cao *et al.* (2008); [b]averages of 1999/2000–2003/04 annual winter counts (Li & Mundkur 2004, 2007); [c]data from Jia *et al.* (2016); [d]average of wintering counts in 2019 and 2020; [e]average of wintering counts from 2015/16–2019/20; [f]average of wintering counts from 2014/15–2018/19; [g]based on new population estimates of Chinese and Japanese wintering populations in 2020.

Table 4. Summary of the results from the regression models of the linear trends in counts for China, South Korea and Japan for Bewick's Swans. ACS = autocorrelation structure (no. of years) included in regression model.

Country	ACS	Parameter	Estimate	s.e.	*t* value	*P* value	Efron's R^2
China	0	Intercept	–7.297	18.109	–0.403	0.694	–
		Year	0.006	0.009	0.666	0.518	0.0357
South Korea	2	Intercept	196.457	15.809	12.427	< 0.001	–
		Year	–0.097	0.008	–12.321	< 0.001	0.805
Japan	7	Intercept	–70.110	9.467	–7.405	< 0.001	–
		Year	0.0372	0.005	7.834	< 0.001	0.834

incomplete, with just *c.* 64,000 in east China, we suggest that the Chinese-wintering part of the population has declined since the 1990s.

Bewick's Swans wintering in Japan have shown an 8,400% increase from 542 in January 1970 to 45,541 in January 2019 (Table 4, Fig. 4, Supporting Materials Table S2). This reflects a significant growth in numbers between winters 1969/70 to 2003/04, with relatively stable numbers since then (Fig. 4).

In summary, the East Asian Continental flyway currently consists of *c.* 65,000 Bewick's Swans with decreasing trends between the 1990s and 2020, whilst the West Pacific flyway consists of *c.* 40,000 Bewick's Swans with increasing overall trends from 1970 to 2019.

Key wintering sites in China and Japan

Based on recent (winters 2015/16–2019/20) survey data, there were 17 key wintering sites (supporting ≥ 1% of the flyway population) in the Yangtze River floodplain for the East Asian Continental flyway, including six sites holding > 5% of the total flyway population (Fig. 5, Supporting Materials Table S3). This compares with just eight key wintering sites identified from the 2003/04 to 2004/05 wintering surveys, which included four sites supporting > 5% of all swans counted in the flyway (Table 5). In recent years, Bewick's Swans in China have wintered mainly in Poyang, Longgan, South Dongting, Tuandun, Taibo and Shijiu Lakes, where maximum numbers exceeded the 5% criterion (3,250 birds), with other key site concentrations at East Dongting, Wang, Futou, and Wuchang Lakes, occasionally at Huanggai, Taibai, Chi, Haikou, Chen, Huangda, and Shengjin Lakes (Fig. 5, Supporting Materials Table S3). In 2003/04 and 2004/05, most birds (98%) wintered in Poyang and Anhui Lakes, with fewer numbers at Wang and Saicheng Lakes during that period (Fig. 2, Table 5).

Bewick's Swans wintering in China have changed their distribution over the last 15 years. Most key sites in Anhui Lakes no longer hold substantial numbers of

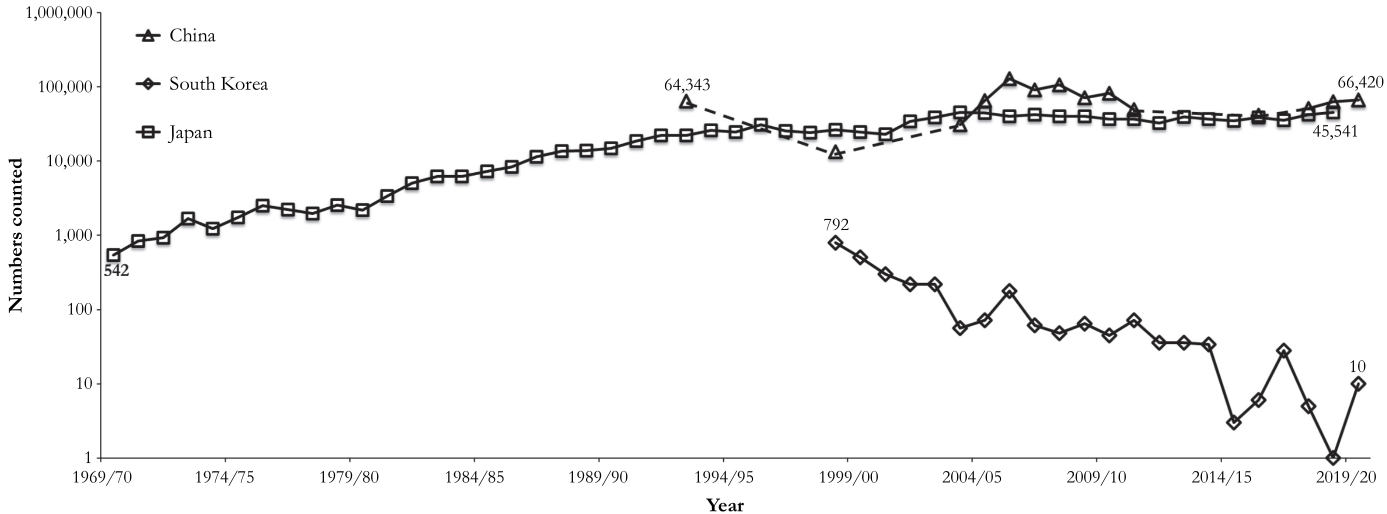

Figure 4. Abundance estimates and trends in numbers of Bewick's Swans recorded in China, South Korea and Japan, based on counts in winters 1969/70 to 2019/20. Totals for Japan and South Korea are derived from national monitoring programmes; Chinese estimates during 1988/1989–2010/11 are from Jia *et al.* (2016), and those from 2011/12–2019/20 based on winter surveys. Count totals are given for the earlies and latest year of wintering survey sequences in each country (also shown in full in Supporting Materials Table S2). Dashed lines denote periods of missing counts in corresponding years.

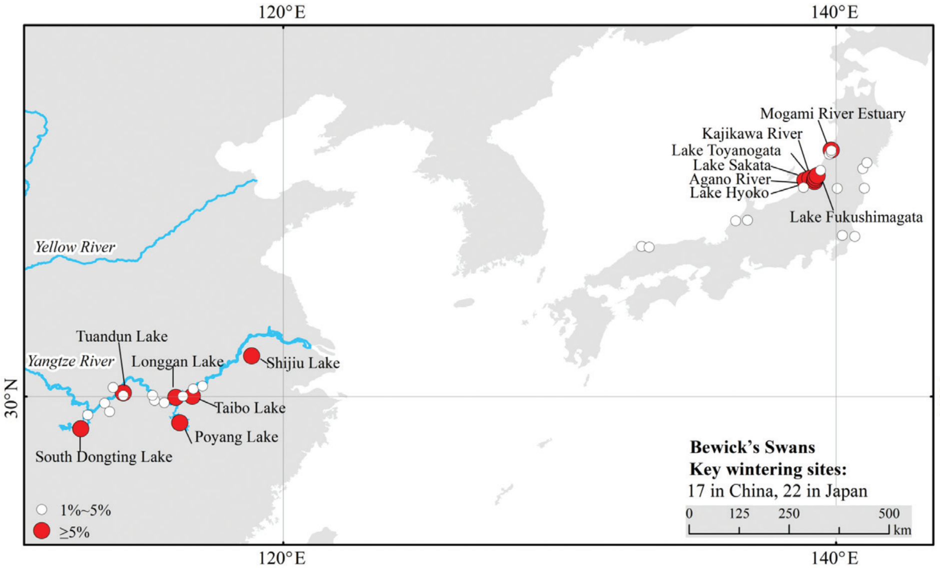

Figure 5. Map showing the 39 key wintering sites identified for Bewick's Swans on the two flyways in East Asia. These include 17 key sites (six 5% key sites and 11 1% key sites) in the wintering range of the East Asian Continental flyway (China), and 22 key sites (seven 5% key sites and 15 1% key sites) in the wintering range of the West Pacific flyway (Japan). The Bewick's Swan is on the verge of extinction as a wintering species in South Korea, so no key site was forthcoming for this wintering group. The 1% and 5% thresholds for key sites were based on maximum numbers recorded for each flyway (1% threshold = 650 swans for the Chinese-wintering and 400 for Japanese-wintering populations; 5% threshold = 3,250 swans for the Chinese-wintering and 2,000 for Japanese wintering populations) during winter surveys in 2015/16 to 2019/20 (also see details in Table S4). The white and red circles indicate the numbers counted as a proportion of the total numbers counted in China or Japan that winter.

wintering swans, whereas larger numbers now occur on other lakes in Hubei, Hunan and Jiangsu Provinces (Fig. 2, Table 5). Wintering numbers of Bewick's Swans at various Anhui Province lakes, including Huangda, Wuchang, Shengjin, Baidang and Fengsha Lakes, declined after 2011/12. Numbers wintering on some Hubei Province lakes increased from 2015/16, especially at Longgan Lake. Similarly, numbers of birds wintering on East Dongting and South Dongting Lake in Hunan Province increased from 2017/18, while Shijiu Lake (Jiangsu Province) has also become a key site for Bewick's Swans in recent years, although this site lacked survey data before January 2016. Poyang Lake has always supported the largest concentrations of swans wintering in China, and together with the Anhui Lakes supported 98% of wintering Bewick's Swans during 2003/04 and 2004/05. However, in winters 2017/18 and 2018/19, while 80% of the swans congregated on Poyang and Longgan

Table 5. Annual maximum counts of Bewick's Swans at key wintering sites for the species (n = 17) in China during December to the following February in winters 2003/04–2019/20. There were six key sites among 12 sites surveyed during winter 2003/04 (including two 1% key sites and four 5% key sites) and 12 key sites among the 17 key sites surveyed during winter 2019/20 (including seven 1% key sites and five 5% key sites). Bewick's Swans were mostly found at Poyang Lake and the Anhui Lakes up until 15 years ago, but since then they have wintering mainly at Poyang, Longgan, Taibo and South Dongting Lakes, and also occasionally at Tuandun and Shijiu Lakes, while numbers using the Anhui Lakes have declined.

ID	Provinces	Wetlands	2003	2004	2006	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	Maximum
C1	Jiangxi	Poyang Lake	13,021	42,843	–	–	–	–	–	–	–	–	8,378	24,641	30,508	14,272	43,974	19,725	43,974
C2		Taibo Lake	–	0	–	–	–	–	–	–	–	–	–	0	–	913	575	3,580	3,580
C3		Saicheng Lake	1,425	0	–	–	–	–	–	–	–	–	–	0	–	0	71	0	1,425
C4	Hubei	Longgan Lake	0	0	–	–	–	–	–	–	–	–	–	13,235	10,156	19,324	7,585	12,658	19,324
C5		Tuandun Lake	–	–	–	–	–	–	–	–	–	–	–	0	–	1,410	2	8,511	8,511
C6		Wang Lake	2,516	257	–	–	–	–	–	–	–	–	–	590	–	1,067	62	1,119	2,516
C7		Futou Lake	–	0	–	–	–	–	–	–	–	–	–	–	0	540	1,002	961	1,002
C8		Chen Lake	0	0	–	–	–	–	–	–	–	–	–	263	–	437	300	779	779
C9	Anhui	Baidang Lake	4,400	8,760	–	21	–	28,450	12,440	17,181	193	3,901	212	12	0	113	48	50	28,450
C10		Wuchang Lake	3,980	2,447	–	29	–	2,521	15,387	0	432	2,183	183	430	73	1,612	152	657	15,387
C11		Fengsha Lake	987	2,056	–	15,000	–	468	233	28	0	0	7	0	36	4	0	0	15,000
C12		Shengjin Lake	4,333	5,429	–	1,007	1,788	2,443	449	1,663	1,126	368	791	298	845	348	207	931	5,429
C13		Huangda Lake	83	2,405	–	–	–	–	–	–	–	–	7	34	–	1,188	65	135	2,405
C14	Hunan	South Dongting Lake	5	0	–	–	–	–	–	–	–	–	–	0	–	1,532	4,107	463	4,107
C15		East Dongting Lake	14	390	172	–	138	102	205	–	–	–	–	29	0	2,713	695	1,897	2,713
C16		Huanggai Lake	–	0	–	–	–	–	–	–	–	–	–	445	–	178	0	2,435	2,435
C17	Jiangsu	Shijiu Lake	–	–	–	–	–	–	–	–	–	–	–	987	–	51	2,883	8,141	8,141

Lakes, more extensive surveys of wetlands with wintering swans found more sites exceeding the 1% criterion, and also more sites supporting swans at all, compared to earlier surveys dating back to 2004 (Table 6). These two pieces of evidence, taken together, show a greater dispersal of Bewick's Swans to more and different wintering sites during these years.

There were 22 key sites used by Japanese-wintering Bewick's Swans from the West Pacific flyway based on recent survey data (winters 2015/16–2018/19), including seven sites holding > 5% of the total flyway population (Fig. 5). Most were distributed in the Mogami River estuary in Yamagata Prefecture, and at Kajikawa River, Lake Toyanogata, Lake Sakata, Agano River, Lake Hyoko and Lake Fukushimagata in Niigata Prefecture (Fig. 5, Supporting Materials Table S3). Most key wintering sites were distributed along both coasts of Japan.

Discussion

A combination of new tracking and winter survey data, combined with the knowledge of Bewick's Swan experts in East Asia, has enabled us to revise and update information on the swans' breeding and wintering distribution, location of key sites and trends in numbers for the Eastern Bewick's Swan population. In particular, two distinct flyways were described for the first time, for Bewick's Swans migrating between breeding areas in the Russian arctic and wintering grounds in East Asia.

Breeding and wintering range

Assessment of the distribution data drew us to the conclusion that current maps illustrating the breeding and wintering ranges of this species should be modified. The breeding range described by BirdLife International and Handbook of Birds of the World (2019) shows it extending into the taiga region for breeding, which is erroneous, and we propose retaining only the Russian arctic and tundra biotope as the breeding distribution, as previously suggested by Cramp & Simmons (1977), on describing the circumpolar distribution for *Cygnus columbianus* (Bewick's and Whistling Swans). This decision is based on published literature (Syroechkovski & Evgeny 2002; Poyarkov *et al.* 2011), and the telemetry data from tagged Bewick's Swans, which clearly showed that they mainly used tundra habitat and almost never summered in taiga immediately south of the tundra. Summer movements of GPS-tagged Bewick's Swans indicated that the species was conspicuously confined to river mouths and adjacent coasts, such as those of the Pur, Taz, Lena, Yana, Indigirka, Kolyma and Palyavaam Rivers (Fig. 1). Bewick's Swans from the Northwest European population similarly favour the coastal bays and adjacent tundra beyond the Pechora River delta (Griffin *et al.* 2016). Given the distinct flyways used by birds from different breeding and wintering areas, described by our tracking data, we further recommend recognising two subpopulations within the Eastern Bewick's Swan population: the "East Asian Continental" subpopulation and the "West Pacific" subpopulation. The migration tracks presented here illustrate the different summer quarters and migration pathways used by Bewick's Swans wintering in China and Japan.

Table 6. Summary table of wetlands surveyed in the Yangtze River floodplain which supported Bewick's Swans during six simultaneous surveys (2003/04, 2004/05, 2015/16, 2017/18–2019/20) in January–February, showing the numbers and proportions of this species counted at each. Out of a total of 41 surveyed wetlands in the 2003/04 wintering survey, 14 wetlands were found to support Bewick's Swans, two (14%) of which supported ≥ 1% of numbers counted in China (*i.e.* qualified as key wintering sites) and five (36%) were 5% key wetlands. Increased survey coverage based on satellite tracking data resulted in a total of 76 wetlands being surveyed in 2019/2020 when 34 wetlands were found with Bewick's Swans, including 7 (21%) 1% key wintering sites and five (15%) 5% key wetlands. The percentage of total surveyed wetlands with Bewick's Swans is the proportion of the total number of wetlands with this species in relation to the total number of wetlands surveyed.

Winter	Yangtze River			Wetlands with BS			Total number of BS counted
	Total no. wetlands surveyed	No. wetlands surveyed with no BS	No. wetlands surveyed with BS	Wetlands with < 1% of BS counted (< 650 birds)	Wetlands with 1%–5% of BS counted (650–3,250 birds)	Wetlands with ≥ 5% of BS counted (> 3,250 birds)	
2003/04	41	27	14 (34%)	7 (50%)	2 (14%)	5 (36%)	30,925
2004/05	75	61	14 (19%)	8 (58%)	3 (21%)	3 (21%)	65,114
2015/16	73	51	22 (30%)	19 (86%)	1 (5%)	2 (9%)	41,741
2017/18	83	54	29 (35%)	17 (59%)	10 (34%)	2 (7%)	51,201
2018/19	79	49	30 (38%)	24 (80%)	3 (10%)	3 (10%)	63,707
2019/20	76	42	34 (45%)	22 (65%)	7 (21%)	5 (15%)	66,420

According to the data available, the breeding origin of the Chinese-wintering birds covers the tundra zone from the western Yamal Peninsula to the Svyatoy Nos Cape (*c.* 2,600 km along the arctic coast, and seemingly including the Lyakhovskie Islands), updating and improving considerably our knowledge of the breeding range. The GPS-tracking data also confirmed information from survey counts, namely that the Chinese wintering range is now concentrated mainly on the middle and lower Yangtze River floodplain. The previously described loss of wintering areas in the southern provinces of China and in the coastal regions may be due to major habitat loss there (Cao *et al.* 2010; Cong *et al.* 2011).

The breeding origin of Bewick's Swans wintering in Japan extends in the tundra zone from the Indigirka River to presumably Koluchin Bay (extending over *c.* 1,600 km; however, our tracked swans went as far east as Pegtymel River, 174°1'E), in accordance with previous knowledge (Solovyeva *et al.* 2019). Further tracking of swans marked in Japan and China and also at different sites in Russia is required, however, to confirm their migration routes, identify any shifts in winter distribution (*e.g.* cold weather movements between countries), and to investigate with larger sample sizes the possibility of overlap in the breeding range of birds from different wintering areas. Our unfortunate lack of migration studies for the small (and now possibly extinct) number of Bewick's Swans wintering in South Korea, precludes any understanding of their breeding range and migration routes, which would benefit from telemetry studies. We postulate that according to geographical evidence, it was closely linked to the population wintering in Japan. Given the apparent ecological isolation of swans from the Chinese and Japanese wintering areas, it is logical to combine tracking studies with molecular methods to verify the division of populations indicated by our telemetry data.

Bewick's Swan flyways in East Asia

For swans wintering in China, the Yamal–China and Lena–China migration routes have previously been described through successful tracking of nine individuals (Huang *et al.* 2018; Vangeluwe *et al.* 2018). In this study, we determined the migratory range of Chinese-wintering Bewick's Swans from a larger sample size, which also enlightened us about a few birds, which showed abnormal migrations. Three birds (bs001 of unknown age and sex; juvenile bs004 of unknown sex; female bs005 of unknown age) summered in the southern taiga/steppe zones, in Mongolia and Inner Mongolia, of which only bs005 was known to have migrated to the Yamal breeding area the following summer. Neither of the other two devices provided information in subsequent years. These birds may potentially have been from the Yamal or Lena breeding areas, but chose to moult south of their normal breeding areas. This phenomenon needs to be supported by field observations to attain a full and adequate explanation. For swans wintering in Japan, our tracking data were consistent with previous ringing and tracking studies in the Chaun Delta (Kondratiev 1984; Higuchi *et al.* 1991) and satellite tracking showed that the swans wintering in Japan are breeding on the tundra, centred around the Kolyma River Delta (Chen *et al.* 2016). None of the juvenile swans from the West Pacific flyway tracked from their breeding grounds in the Chaun Delta, summered further south in the taiga forest zone, although the sample size ($n = 3$) was very small.

Despite the large numbers of tagged birds that provided migration tracks, the number and distribution of our capture sites remained limited, potentially introducing bias into the study of Bewick's Swan migration in East Asia. The arctic landscape and logistic limitations greatly restrict swan capture sites to known summer areas, but catching swans at other sites would extend the utility and reliability of the results. One key task is to track the migration of swans breeding between Svyatoy Nos Cape and the Indigirka Delta, to determine the degree of potential overlap between the Chinese- and Japanese-wintering populations on the summering areas. Tracking of Bewick's Swans from the Yamal Peninsula revealed that swans from this area migrated diversely to the eastern Mediterranean Sea, the Caspian Sea area and to China (Vangeluwe *et al.* 2018). Rozenfeld *et al.* (2019) speculated that some of the birds summering in the Nenetsky Autonomous Okrug (west of Yamal) are swans of Asian origin, which have expanded their range westwards. Certainly, increased sample sizes of tracked swans will help to provide better information on the degree of overlap in the summering ranges of the Caspian- and Chinese-wintering elements of the Bewick's Swan population.

Abundance and trends among wintering populations

We also sought to update the estimate of population size and trends in Bewick's Swans wintering in three countries in East Asia in recent winters (2011/12–2019/20). Wintering population estimates based on incomplete surveys in the 1990s, and comprehensive surveys made in the early 2000s, suggest a decline of Bewick's Swans in the region. Numbers wintering in China apparently decreased during 2004/05 to 2019/20, perhaps due to habitat degradation in the MLYFP (Jia *et al.* 2019), although fluctuations within this trend may be attributable to different survey coverage over the years and the errors involved with estimating total numbers from these. In winters 2011/12–2014/15 and 2016/17, only the key Bewick's Swan wintering sites were covered in China, so we cannot estimate the Chinese totals for these years. The increase in numbers in winters 2018/19 and 2019/20 will have been partly due to increased survey coverage, resulting from information coming from the tracking study.

Numbers of Bewick's Swans wintering in South Korea, although always relatively small, have shown a downward trend for many years. In the absence of ecological research on the species, the reason why the birds have declined here is unknown, but the Bewick's Swan appears to be on the brink of extinction as a regularly wintering species in the country.

Japanese-wintering numbers increased from the 1970s, primarily because Japan has had a long tradition of providing rice and bread to swans (Albertsen & Kanazawa 2002; Shimada & Mizota 2011). During the first ten years (1970–1980), however, the increase in wintering numbers is thought to be also attributable to: 1) Whooper Swans and Bewick's Swans not being treated as separate species at survey sites, and 2) increased survey coverage during this period resulting from improved knowledge of the swans' wintering sites (Albertsen & Kanazawa 2002). There remain some species identification errors associated with the Japanese swan monitoring data even in recent years. This is because local governments do not always consult with birdwatching organisations and may ask inexperienced observers to undertake the monitoring. A future priority remains to reduce this potential level of survey error by ensuring that experts and experienced observers conduct the winter surveys, and by providing training to new recruits. Solovyeva *et al.* (2019) found that the reproductive success rate in the Chaun Delta was regulated by density-dependence, which may contribute to explaining the stability in the Japanese-wintering population in recent years. However, the breeding areas used by Chinese-wintering swans lack long-term monitoring, so establishment of research programmes in these areas would also help to elucidate and interpret trends in Chinese-wintering numbers.

Current research focused on the Eastern populations should increasingly be combined with those of the Caspian and Northwest European wintering swans, to compare and contrast population changes and gain insight into their causes. Telemetry tracking studies should also be undertaken to determine whether and to what extent there is interchange of individuals between sympatric-breeding swans on the Yamal Peninsula, providing a possible explanation for the decline of wintering populations in China.

Key wintering sites of Bewick's Swans in China and Japan

As Bewick's Swans in East Asia were identified to Chinese and Japanese winter quarters, based on their satellite tracking data, this study was able to update the list of key wintering sites for Bewick's Swans in China and Japan. Compared with the 1% criterion from Wetlands International (2019) for Bewick's Swans in East Asia, the 1% criteria for Chinese and Japanese populations are slightly smaller, because they are based on only a part of the total East Asian Bewick's Swan population, resulting in more key wintering sites reported for Japan. Bewick's Swans are concentrated in the middle and lower Yangtze River floodplain in China, mostly occurring in natural wetlands, including Poyang, Longgan, South Dongting, Tuandun, Taibo and Shijiu Lakes during the wintering period. Bewick's Swans wintering in Japan likewise feed mainly in wetlands, but also rely upon farmland. Yu *et al.* (2017) showed that Chinese-wintering geese are slow to shift from natural wetlands to farmland habitat, and future research should combine GPS tracking data and remote-sensing data to analyse the differences in habitat use between Chinese- and Japanese-wintering swans. Results could then assess the energetic benefits of foraging in these different types of habitats in the two countries.

Key sites for Bewick's Swans in the Yangtze River have changed substantially since 2010. Before 2010, 90% of swans were counted on the Anhui Lakes and at Poyang Lake in Jiangxi, with fewer than 3,000 counted in Hunan and Hubei (Barter *et al.*

2004, 2006). After 2010, most swans were counted at Poyang, Longgan and Dongting Lakes, while the number on the Anhui Lakes reduced significantly. The decrease in numbers, at the Anhui Lakes may be due to the collapse of submerged vegetation *Vallisneria* sp. associated with the development of aquaculture (Cong *et al.* 2011; Fox *et al.* 2011). Aquaculture in Wang and Saicheng Lakes may also have contributed to the decrease in the number of swans there, as elsewhere in the Anhui Lakes. The number of Bewick's Swans at Dongting Lake increased, but this was partly because the coverage of the wintering surveys was expanded based on results from the swan satellite tracking data. The increased survey coverage may also explain the increasing bird numbers counted at Taibo Lake. The increase in the numbers of swans wintering at Longgan, Chen and Futou Lakes in Hubei Province may be due to the improved management at these lakes, many of which have benefitted greatly from the recent strengthened emphasis upon nature conservation. Because survey data for Shijiu and Tuandun Lakes have been lacking until recently, the changes in swan abundance at these lakes remain unclear. In the longer term, satellite tracking studies of swans using newly identified key sites should be a target for research, to elucidate the behavioural changes and habitat use by Bewick's Swans frequenting these lakes, so we can be in a better position to apply effective conservation measures for their well-being at these poorly known locations. Future research should also include long-term monitoring, energetics analyses linked to habitat use and feeding behaviour studies, and assessment of how hydrological management affects submerged vegetation in lakes, in order to confirm reasons underlying the observed changes in distribution of Bewick's Swans at key sites in China.

Management recommendations

In order to understand the distribution, abundance, important habitats and bottlenecks in the annual cycle of Bewick's Swans in East Asia, it is necessary to unite Russia, Mongolia, China, South Korea and Japan, as well as countries of the Middle East and Europe, in establishing a long-term coordinated scientific monitoring system. For the declining element of the population, especially among those swans wintering in China (the largest wintering numbers in East Asia), protection of the remaining good quality habitats for Bewick's Swans along the migration routes and throughout their wintering range is crucial, with important sites located by a combination of satellite tracking and field surveys. Further research on mortality and reproductive success rates should be added to assess population trends and provide a scientific basis for species conservation, especially in light of the decision to down-list the species in the Russian Red Data Book since 2020 (Ministry of Natural Resources of Russian Federation: # 162 from 24/03/2020), which allows the potential for hunting of the species in its eastern flyways.

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Appendix 1. Ten experts from five countries participated in the discussion of the distribution and migration routes of the Eastern Bewick's Swan population.

No.	Name	Nationality	Institute
1	Sonia B. Rozenfeld	Russian	Bird Ringing Centre of Russia
2	Anton Sasin	Russian	Amur Regional Public Environmental Organisation "AmurSEU"
3	Inga Bysykatova-Harmey	Russian	Institute for Biological Problems of Cryolithozone, Siberian Division of Russian Academy of Sciences (IBPC, SDRAS)
4	Oleg Goroshko	Russian	Daursky State Nature Biosphere Reserve
5	Diana Solovyeva	Russian	Institute of Biological Problems of the North
6	Han Soo Lee	South Korean	Korea Institute of Environmental Ecology
7	Nyambayar Batbayar	Mongolian	Wildlife Biologist, Wildlife Science and Conservation Center, Mongolia
8	Sachiko Moriguchi	Japanese	Nippon Veterinary and Life Science University
9	Lei Cao	Chinese	Research Centre for Eco-Environmental Sciences, Chinese Academy of Sciences
10	Xin Wang	Chinese	Research Centre for Eco-Environmental Sciences, Chinese Academy of Sciences