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Article *in* Wildfowl · January 2021

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Abstract

Telemetry data, wintering waterbird surveys and expert knowledge are used here to describe the links between the summer and winter distributions of the Swan Goose *Anser cygnoides* in East Asia, and to determine the status of the species. Updated information suggests the existence of at least two discrete migratory flyways in the region: an "Inland flyway" and a "Coastal flyway". The Inland flyway consists of birds that summer in Mongolia, the Durian steppe and northeast China, extending east to Khanka Lake in far eastern Russia. These geese winter in the Yangtze River floodplain in China, congregating at Poyang and Shengjin Lakes. Total wintering numbers for this group of birds were estimated at *c.* 54,400 in recent years, a decline from *c.* 78,000 in the early 2000s. Birds of the Coastal flyway seem discrete from those following the Inland flyway and occur further east, spending the summer at Udyl Lake and northern Sakhalin Island in Far East Russia. They migrate to winter mainly on the Minjiang River estuary (Fujian Province, China), with a few remaining to winter in South Korea. About 400 Swan Geese have been counted in the Coastal flyway population in recent years, and, following declines from 800 in the early 2000s, it is thought that they currently face extinction. Our results highlight that urgent and effective conservation efforts are needed to protect this declining population of a globally threatened species, especially those wintering in Korea and the Minjiang Estuary. New data provide a scientific basis for the conservation of this species in the region, but also highlight the need for improved monitoring and management of the declining numbers wintering in China.

Key words: distribution, East Asia, migration routes, population trends, Swan Goose.

Endemic to East Asia, the Swan Goose *Anser cygnoides* is estimated to number *c.* 60,000–90,000 individuals and since 2008 has been listed as globally vulnerable in the International Union for Conservation of Nature Red List of Threatened Species (BirdLife International 2020a,b). The breeding distribution of the species extends from western Mongolia to Sakhalin Island in Far East Russia, with an estimated *c.* 43,000 birds in the core breeding areas in Mongolia, adjacent parts of Russia and northeast China (Fox & Leafloor 2018; BirdLife International and Handbook of the Birds of the World 2019). One hundred years ago, the wintering range of the Swan Goose extended to Japan and Korea (Fox & Leafloor 2018), but during the last 30 years, the species has contracted its winter distribution to be almost exclusively confined to China, with very few birds now reported in South Korea and Japan (Kear 2005; Jia *et al.* 2016). The species was formerly widely distributed throughout the Yangtze River floodplain (occurring in five provinces and in Shanghai City) and extending along the Jiangsu coast before 1996 (Cao *et al.* 2008b). However, since 2004, the majority

of the Swan Geese have been confined to wintering areas in Jiangxi and Anhui Provinces (Barter *et al.* 2004, 2005; Cao *et al.* 2010; Zhang *et al.* 2011), with some 800 additional birds frequenting the estuary of the Minjiang River, in the Fujian Province of China (Barter 2007). Until 2016, the geese were mostly concentrated in Poyang Lake, although wintering numbers occurred throughout the Yangtze River floodplain. More recently, however, numbers have declined markedly in Anhui Province (An *et al.* 2019). Overall, therefore, the globally threatened Swan Goose seems to have contracted its winter range quite radically, a trend that has continued within China, and it now has a much narrower distribution at a few lakes in the Yangtze region although still with a disjunct group on the Minjiang River estuary (Zhang *et al.* 2011; Jia *et al.* 2016).

Swan Geese rely almost totally on natural wetlands throughout their annual cycle. However, many of the wetland systems upon which they rely are facing serious threats from severe climate change, drought, land reclamation, grass-fires, and anthropogenic disturbance. These problems have been described from the breeding and moulting areas in Mongolia and adjacent parts of Russia and Inner Mongolia, China (Goroshko 2001, 2003; Goroshko & Liu 2003; Goroshko 2004; Tseveenmyadag *et al.* 2007; Goroshko 2012; Batbayar *et al.* 2013; Goroshko 2015; Tao *et al.* 2015; Choi *et al.* 2016b). Additionally, the species faces serious habitat loss at its staging sites, especially in northeast China (Xu *et al.* 2019, 2020). Illegal hunting is also a significant threat to the geese in Russia (Goroshko 2001; Poyarkov 2005; Goroshko 2012) and the species has suffered from habitat degradation throughout the wintering range (Wang *et al.* 2017). At the Yangtze wintering resorts, Swan Geese dig for overwintering Tape Grass *Vallisneria* sp. tubers buried in the substrate, which are successively exposed in the soft mud during the autumn and winter following water level recession (Zhang & Lu 1999; Fox *et al.* 2011; Chen *et al.* 2019). This makes the geese highly sensitive to water level fluctuations, which in recent years has had an adverse effect on their feeding opportunities (Aharon-Rotman *et al.* 2017). Not only have the construction of new dams interfered with seasonal changes in wetland water levels, but aquaculture and pollution have also added to reductions in food availability (Fox *et al.* 2011; Chen *et al.* 2019), compounding effects that are thought to have contributed to the contraction in the historically wider distribution of Swan Geese in eastern China into the last remaining fragments of suitable habitats in the region.

Telemetry studies have made a major contribution towards the description of Swan Goose migration routes in recent years. Satellite tracked birds from eastern Mongolia migrated to stopover sites at the Yalu River estuary and Taeryong River estuary in North Korea, where they remained for several weeks before moving to their wintering grounds in the Yangtze River floodplain in China (Batbayar *et al.* 2013). However, almost nothing was known about the migration routes taken by Swan Geese that breed in mid- and western Mongolia, northeast China and in the Amur River region of Russia. In the

case of the latter group of birds, haplotype differences between Russian Swan Geese from the Amur River region of Khabarovsk Krai and those from the Chita region (adjacent to eastern Mongolia) had suggested longer term separation of individuals in their respective breeding areas, and potential differences in their migration pathways and wintering sites (Poyarkov *et al.* 2010).

The current study integrates satellite tracking, wintering waterbird surveys and expert knowledge, to update descriptions of the summer and winter distributions of the Swan Goose, to identify migration flyways for each of the discrete population units, and to estimate current numbers and trends for each wintering population. Such information is important for promoting international cooperation and for the exchange of information required to ensure that the breeding, moulting, staging and wintering habitats critical to this species are protected effectively. The study should also help to improve future monitoring of Swan Geese along its annual migration routes and promote its conservation within the East Asian-Australasian Flyway.

Methods

In October 2019, the "*2nd International Symposium on Developing Effective Coordinated Monitoring of East Asian Waterbirds in the 21st Century*" was convened in Beijing, China. During the symposium, 16 experts from six countries discussed and contributed to the delineation of the summer and winter distributions and to describing migration routes followed by the Swan Goose in East Asia (Supporting Materials Table S1).

Migration data

Telemetry data from Swan Geese fitted with GPS loggers, supported by information gathered from Anatidae experts at the symposium, were used to define the global flyways for the species. In the breeding range, moulting and flightless Swan Goose families were rounded up on lakes using boats and gently pushed into funnelled coral traps on the shore, for ringing and tagging. Staging birds in Korea were caught with cannon nets; wintering birds in China were dazzled by the beams of powerful lamps and then caught by hand nets from boats at night, or in heavy-duty mist-nets (designed for catching large birds) set at their roosts. In total, 363 Swan Geese were caught, including 327 birds at 13 key sites across the summering range, five birds at one key staging site and 31 birds at one key wintering site during winters 2014/2015–2017/18 (Table 1). Two hundred and fifty-nine individuals with at least one complete spring or autumn migration were used to contribute data to identify the flyway corridors (Supporting Materials Table S2, Table 2, see below).

One hundred and twenty-seven of the moulting Swan Geese caught and fitted with GPS transmitters during summers 2014–2018 inclusive were from 12 main sites in Mongolia. These birds were caught at Uvs Lake (50°27'N, 93°6'E) and Taigan Lake (46°21'N, 97°24'E) in western Mongolia in 2017–2018; at Ugii Lake (47°46'N, 102°45'E) in central Mongolia in 2017; and in eastern Mongolia at Baruun Ereen Lake (48°0'N, 112°56'E), Buir Lake (47°38'N, 117°34'E), Galuut Lake (49°44'N, 115°18'E), Bus Lake (49°43'N, 115°9'E), Chukh Lake (49°31'N,

Table 1. Summary table of 363 Swan Geese caught and fitted with solar-powered GPS/GSM telemetry devices in East Asia during 2014–2018, including 327 birds at 13 sites across the summering range, five birds at one key staging site and 31 birds at two key wintering areas, giving the breakdown of age, sex and catch totals for tagged birds at each site.

	Capture sites	Coordinates		Capture period	Age			Sex			Total
		Latitude	Longitude		Adult	Juvenile	Unknown	Female	Male	Unknown	
Summering area (n = 327)	Uvs Lake, western Mongolia	50.44	93.10	2017	2				2		2
	Jiree River, western Mongolia	50.46	93.10	2018	3			3			3
	Taigan Lake, western Mongolia	46.36	97.40	2018	8			3	5		8
	Ugii Lake, middle Mongolia	47.78	102.76	2017	25			8	17		25
	Buir Lake, eastern Mongolia	47.64	117.57	2017	25			10	14	1	25
	Davsan Tsagaan Lake, eastern Mongolia	49.64	114.68	2016	3	5		3	4	1	8
	Baruun Ereen Lake, eastern Mongolia	48.01	112.94	2016	2	2		2	2		4
	Galuut Lake, eastern Mongolia	49.74	115.31	2014–2016	2	9		5	4	2	11
	Bus Lake, eastern Mongolia	49.73	115.15	2014	3	6		4	5		9
	Khaichiin Tsagaan Lake, eastern Mongolia	49.68	114.68	2014	2			2			2
	Gurmen Lake, eastern Mongolia	47.83	112.14	2015			10	5	5		10
	Chukh Lake, eastern Mongolia	49.53	114.66	2014–2016	7	11	2	6	11	3	20
	Hulun Lake, Inner Mongolia	48.34	117.47	2017	200			84	90	26	200
Staging site (n = 5)	Jianghua Bay, South Korea	37.28	126.77	2015			5			5	5
Wintering area (n = 31)	Anhui Lakes, Yangtze River	30.9	117.67	2015–2016	1	1		2			2
	Poyang Lake, Yangtze River	29.12	116.27	2015–2016	9		20	11	18		29

Table 2. Summary of the satellite tracking data derived from 259 Swan Geese tagged between 2014–2018, which formed the basis for describing two international flyways. A total of 218 spring and 409 autumn tracks include 215 spring and 409 autumn tracks of 256 birds of the Inland flyway, which were caught in the main summering area (western, central and eastern Mongolia, Hulun Lake) and wintering area (the Yangtze River floodplain). Tracks along the Coastal flyway, were from three birds caught at a key spring staging site (Jianghua Bay).

Flyways	Capture sites	Tracking period	No. of individuals	Spring	Autumn	Migration routes
Inland flyway	Western Mongolia	2017–2019	10	3	11	West Mongolia–Yangtze River
	Central Mongolia	2017–2019	18	13	29	Central Mongolia–Yangtze River
	Eastern Mongolia	2014–2019	49	32	70	Daurian steppe–Yangtze River
	Hulun Lake	2017–2019	169	156	297	Daurian steppe–Yangtze River
	Yangtze River	2015–2018	10	11	2	West Mongolia/Daurian steppe–Yangtze River
	Flyway total	**2014–2019**	**256**	**215**	**409**	
Coastal flyway	Jianghua Bay	2015	3	3		Udyl Lake–Minjiang Estuary
	Flyway total	**2015**	**3**	**3**		
Overall total			**259**	**218**	**409**	

114°39'E), Davsan Tsagaan (49°38'N, 114°40'E), Khaichiin Tsagaan Lake (49°40'N, 114°40'E) and Gurmen Lake (47°49'N, 112°8'E) in 2014, 2016 and 2017. In addition, 200 were caught at Hulun Lake, Inner Mongolia (48°20'N, 117°28'E) in China in 2017. Thirty-one Swan Geese were also caught at Poyang Lake (29°07'N, 116°16'E) and the Anhui Lakes (30°54'N, 117°40'E) in the Yangtze River floodplain from 2015 to 2017 during the wintering period. Five Swan Geese were caught at key staging sites at Jianghua Bay in South Korea (37°17'N, 126°46'E) in March 2015.

Birds were fitted with different neck collar or backpack solar-powered transmitters (Druid tech, China, weight = 35 g or 45 g, mounted on neck collars; Hunan Global Messenger Technology Company "HQXS", China, 24 g, mounted on backpacks; KoEco, South Korea, 50 g, using backpacks; Ornitela, Lithuania, 45 g, mounted on neck collars; and Ecotone, Poland, 30 g mounted on neck collars or 53 g backpacks). All recorded GPS positions and transmitted data were downloaded via the GSM mobile phone networks. The transmitters provided 32 ± 57 (mean ± s.d., range = 3–914) GPS positions per day, contingent upon power supply (Supporting Materials Table S2). First-day movement data after birds were captured and last-day data before birds died or lost contact, were excluded from all analyses. Birds were considered to have died if the tracking data showed > 1 of the following states: (1) birds remained in an area within a diameter of < 50 m for 5 days, (2) the tri-axial acceleration was parallel in two axes, with net movement of zero, (3) temperature changes monitored by the transmitter were consistent with the changes of the ambient temperature, and (4) invalid signals were returned for a prolonged period.

Distribution and migratory range

The global distribution of the Swan Goose described in the maps developed by BirdLife International and Handbook of the Birds of the World (2019) were incorporated into ArcGIS 10.2 (ESRI 2013). We then updated these maps in line with data from Fox & Leafloor (2018), from counts made of Swan Geese in their wintering range (see *Methods* below), from information on the migration routes and the winter/summer distributions derived from the satellite tracking data (see *Methods* above) and from expert knowledge pooled at the Beijing Symposium.

Abundance estimates and population trends

The wintering range of the Swan Goose extends over three countries – China, South Korea and Japan – and each has its own methods for assessing the numbers of waterbirds present nationally during winter. It is expedient here to assess variation in Swan Goose winter abundance at the national level.

Data on the numbers of Swan Geese wintering in the Yangtze River floodplain prior to winter 2011/12 were derived from Jia *et al.* (2016). This was supplemented in 2003/04, 2004/05, 2015/16, 2017/18, 2018/19 and 2019/2020 with counts from synchronous Yangtze waterbird surveys undertaken during mid-December to early February, which are thought to have covered the vast majority of wintering Swan Geese in China (Cao *et al.* 2010; Jia *et al.* 2016).

For Swan Geese wintering on the Minjiang River estuary, Fujian Province in China, survey data from 2002/03 to 2008/09 were extracted from the literature (Yang 2004; Barter 2007; Hong Kong Birdwatching 2009, 2011), and from the more recent annual wintering surveys, which were conducted from December–February each year during 2009/10 to 2019/20 inclusive.

The Korean Ministry of Environment and its associated institutes – the National Institute of Environmental Research (until 2007) and National Institute of Biological Resources (since 2008) – have conducted an annual nationwide census at most lakes, reservoirs and coastal areas known to be important for waterbirds during mid-winter since 1998/99. The simultaneous 2-day field counts, undertaken annually in mid or late January, are conducted by ornithologists, avian researchers, experienced birdwatchers and volunteers to estimate the distribution and abundance of waterbirds spending the non-breeding period in South Korea.

In Japan, annual mid-winter (*c.* 15 January) surveys of waterfowl populations have been conducted by the Ministry of the Environment, with the assistance of prefectural governments, since January 1970. This nationwide survey covers all of the principal sites for swan, goose and duck species wintering in the country (Ministry of the Environment of Japan 2019).

Given the incomplete coverage of Swan Geese wintering in China prior to 2012, we assessed trends in numbers based on the counts and coverage of the Yangtze River survey from 1987/88 onwards (Cao *et al.* 2010; Jia *et al.* 2016). There is increasing evidence that loss of coastal wetlands has reduced numbers of Swan Geese wintering along Chinese coastlines (see later), so we contend that surveys subsequent to 2012/13 will have covered the majority of the recent wintering range, so these data were used to estimate the current total population size for the species. The annual counts recorded during systematic national surveys of waterbirds in South Korea (since the 1990s) and Japan (since 1970), are also used to estimate trends in these wintering populations.

Simple linear regressions were applied to log-transformed annual count data to detect general trends in numbers for Swan Geese in the Yangtze River, the Minjiang River estuary, and in South Korea. Initial exploration of linear regression residuals of temporal trends in the count data for these three areas, fitted using the nlme package (Pinheiro *et al.* 2020), showed only minor evidence of statistically significant residual temporal autocorrelation at time lag 6, and for all other time lags it was not significant ($P > 0.05$). Given the lack of serial residual autocorrelation, no autocorrelation structure was included in subsequent linear regressions.

Swan Goose wintering sites

The current estimate of winter abundance for Swan Geese in the Yangtze River floodplain of China was based on the average of the total numbers counted during surveys made in winter 2018/19 and 2019/20, because these data were considered the most reliable in terms of coverage. For the Minjiang River estuary of China and South Korea, where coverage was more or less consistent in winters 2015/16–2019/20 inclusive, we calculated current wintering numbers as an average of the maximum

counts recorded each winter over the last five years. In each country, key sites were determined from the count data recorded during the 2015/16–2019/20 surveys, and were classified as being those that exceeded 1% of the derived total national estimates at least once, for the corresponding country during this period (Table 3).

Changes in the numbers and distribution of Swan Geese at key sites in China over the past 15 years were investigated by comparing annual maximum counts at these sites from 2004 to 2020. In addition, the survey data of the most important key sites (Poyang Lake, Dongting Lake, Hubei and Anhui Lakes) along the Yangtze River floodplain in winters 2005/06–2014/15 and 2016/17 were also included.

Results

Summering and wintering distribution range

On combining all information currently available, we considered that in summer the

Table 3. Population size estimates and current 1% criteria for determining sites of international importance, for Swan Geese using three wintering areas in two flyways, based on winter survey data (1999/00–2019/20) in the Yangtze River floodplain, Minjiang River estuary and South Korea.

Timing of population estimate	Inland flyway	Coastal flyway		Overall abundance
	Yangtze River	Minjiang River estuary	South Korea	
Population estimate in 2000–2005	78,000[a]	810[b]	18[c]	78,000
Population estimate in 2007–2011	75,000[d]	650[e]	54[d]	76,000
New population estimate in 2016–2020	54,000[f]	368[g]	47[g]	54,400
		420[i]		
New 1% criteria in 2016–2020[j]	540	4		544

Notes: [a] = data from Cao *et al.* (2008a); [b] = February 2006 survey data; [c] = average of the annual winter counts during 1999/00–2003/04 (Li & Mundkur 2004, 2007); [d] = average of the annual winter survey data during 2006/07–2010/11 (from Jia *et al.* 2016); [e] = average of the annual winter counts during 2006/07–2010/11; [f] = new population estimate, determined by averaging the total numbers counted on the Yangtze River in winters 2018/19 and 2019/20; [g] = new population estimate, determined by averaging total numbers counted on the Minjiang River estuary and in South Korea during winters 2015/16–2019/20; [i] = total wintering numbers in the Coastal flyway; [j] = new 1% criterion based on new population estimates of Inland and Coastal flyway counts.

Swan Goose occurs in four main relatively discrete areas. These are: (1) Mongolia, adjacent parts of Russia and northeast China (Inner Mongolia and Songnen Plain); (2) Khanka Lake; (3) the Amur River, Udyl Lake, Ulbansky Bay and northern Sakhalin Island, and (4) the few Swan Geese which summer at Xilin Gol in Inner Mongolia and Kangba Noel in the Hebei Province of China (Fig. 1).

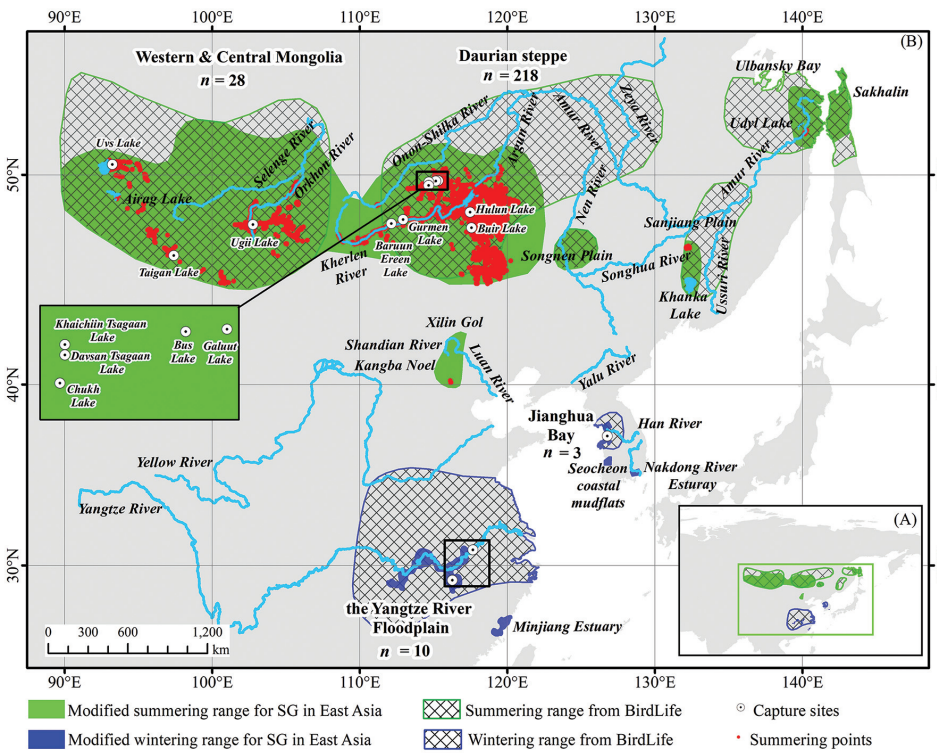

Figure 1. Global distribution of the Swan Goose (A) and enlarged detailed map of its range (B). B illustrates the revised assessment of its distribution: solid green shading = proposed summering areas; blue shading = winter range; and black cross-hatch = previous description of the summer and winter distributions (the latter from BirdLife International and Handbook of the Birds of the World 2019). Revision of the summer distribution was based on tracking data (red dots = GPS locations for each tagged goose between arrival and departure at the summering grounds), expert knowledge and a literature review (including Fox & Leafloor 2018). The revised wintering range was based on field survey data, expert knowledge and information from the literature (*e.g.* Fox & Leafloor 2018); see *Methods* for details. Two hundred and fifty-nine individuals, caught in 12 key areas during summer, a key wintering area (shown by the black box: the Yangtze River floodplain), and at a key staging site (Jianghua Bay), provided tracking data used in the study. Circles with black dots = capture sites, *n* = number of birds that completed at least one spring or autumn migration (Table 2). All the sites/area names mentioned in the paper are shown on the map.

The tracking data showed that the distribution of tagged Swan Geese ranged between Uvs Lake and Airag Lake in the Great Lakes Depression of western Mongolia, lakes in the Tuul and Kherlen River Basin of central Mongolia, lakes in the Onon River and Ulz River Basins, the Argun River, Chukh River, Kherlen River and Buir Lake in eastern Mongolia, and Hulun Lake in Inner Mongolia, China. Small numbers of Swan Geese also occur in the Amur River basin near Udyl Lake in far east Russia. Moulting sites identified by the tracking data included: Zun Torey Lake (Russia), Uvs Lake and Taigan Lake (western Mongolia), Ugii Lake in middle Mongolia, Khukh Lake, Kherhen Lake and Buir Lake (eastern Mongolia), and the Hailaer River, Hui River, Xin Barag Left Banner and Xilin Gol in the Inner Mongolia region of China (Fig. 2).

Although earlier studies found Swan Geese distributed throughout the Yangtze River floodplain in winter (Cao *et al.* 2010), the current wintering range is more concentrated, mainly centred on Poyang Lake and Shengjin Lake, with small numbers on the Minjiang River estuary in recent years (Fig. 1). Few birds winter in South Korea, but those that do are found on the Han River and Nakdong River estuaries and on the coastal mudflats of Seocheon (Fig. 1). Very few Swan Geese now winter in Japan.

Global migration routes

Satellite tracking data from 259 individuals differentiated an "Inland flyway" group of Swan Geese (which migrates of a broad front from its summer haunts in Mongolia, northeast China, and at Khanka Lake (Russia) to wintering areas on the Yangtze

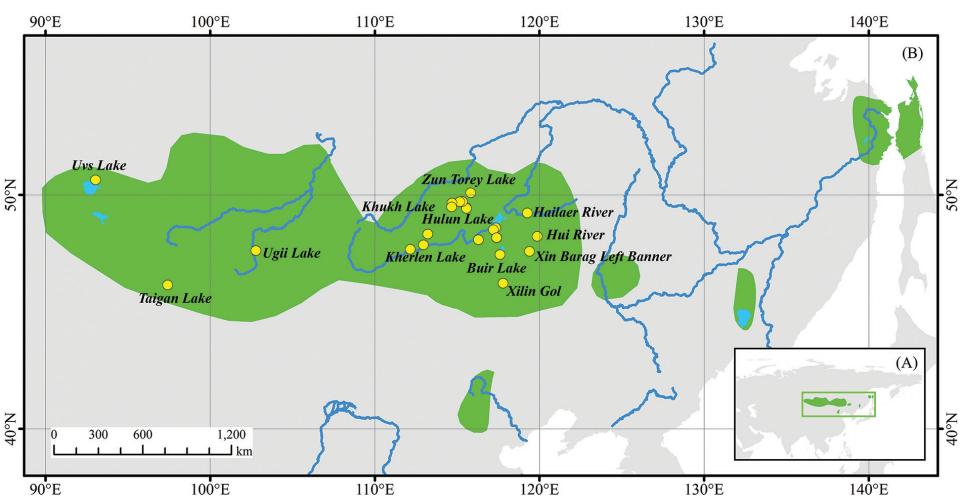

Figure 2. Global distribution of the Swan Goose (A), with moulting sites (yellow dots) shown in the main map (B). Key moulting sites were located in Russia, in western, middle and eastern Mongolia, and in Inner Mongolia, China. Numbers counted at Buir Lake, the largest of the moulting sites, peaked at *c.* 4,000 individuals during the five most recent survey years (*i.e.* in 2016–2020). The moulting site data were from Zhu Qin (unpubl. data).

River floodplain of China) from a "Coastal flyway". The latter consisted of birds that summered at Ulbansky Bay and Udyl Lake in Far East Russia and migrated to South Korea and the Minjiang River estuary of China to winter (Fig. 3).

Description of the Inland flyway was based on the full migration data for 256

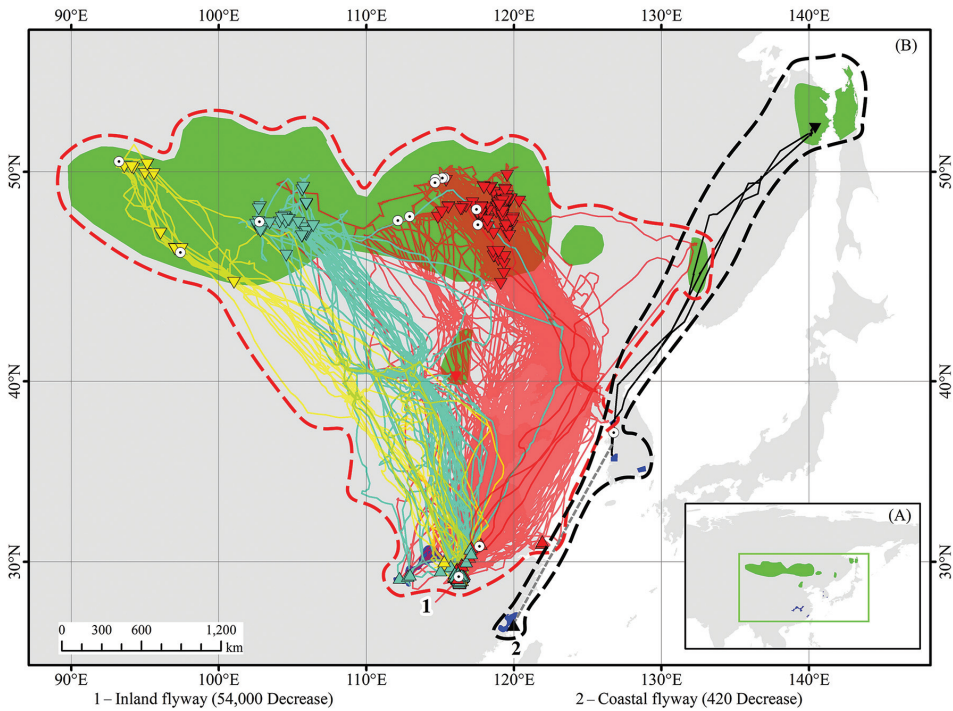

Figure 3. Global distribution of the Swan Goose (A), illustrating the Inland flyway (red dashed line) and the Coastal flyway (black dashed line) in the main map (B). The Inland flyway was described from the migration routes of 257 telemetry-tracked individuals (yellow, turquoise and red solid lines). Individual migration routes followed from different capture sites include Swan Geese caught in western (n = 10, yellow solid lines), central (n = 28, turquoise solid lines) and eastern (n = 50, red solid lines) Mongolia, as well as at Hulun Lake (n = 169, red solid lines) across all summering areas. All of these geese wintered on the Yangtze River floodplain. Of ten wintering birds caught in the Yangtze River floodplain, two (yellow solid lines) summered in west Mongolia and eight (red solid lines) summered in eastern Mongolia. The Coastal flyway is defined by migration routes of three individuals (black lines, and grey dashed line due to a lack of tracking data). Circles with black dots = capture sites; light green shaded areas = our revised suggestion for the summering range; dark blue areas = the revised wintering range. Inverted and regular triangles = breeding/summering and wintering areas used by tracked individual(s), respectively. Flyway population sizes and trends are from the results of this study, based on winter count data from China (1987/88–2019/20) and South Korea (1998/99–2019/20).

individuals (215 spring tracks, 409 autumn tracks, Table 2), which indicated three migration routes – western, central and Daurian steppe migration routes – depending upon where the birds were caught. The western Mongolian migration route was defined by 12 individuals, which provided full migration data (12 autumn and 6 spring tracks). Ten birds were tagged at Uvs Lake and Taigan Lake in western Mongolia, summered in the Great Lakes depression, migrated through western Mongolia and the Yellow River in China, to winter in the Lower Yangtze River floodplain (LYRF). Two birds caught on the Yangtze River floodplain, also migrated to western Mongolia in summer. The central Mongolian migration route was defined by full migration data from 18 tracked individuals (29 autumn and 13 spring tracks) captured at Ugii Lake, which migrated through Inner Mongolia, also wintering in LYRF. Two hundred and twenty-six individuals with full migration data (368 autumn and 196 spring tracks) defined the Daurian steppe migration route. One hundred and sixty-nine of these geese were caught at Hulun Lake in Inner Mongolia and 49 geese in northeast Mongolia. All of these geese migrated through the sandy substrate lakes in Tongliao (Inner Mongolia, China) and via the Yalu River Estuary (on the borders of North Korea and China) to winter in LYRF. A further eight birds captured in the Yangtze River, migrated through the Yalu River Estuary and northeast China, to summer in eastern Mongolia.

Despite their distinct breeding areas, Swan Geese using these migration routes subsequently mixed on their wintering grounds in the LYRF, mainly at Poyang Lake and the lakes in Anhui Province, and so the tracks have been combined to describe the Inland flyway. Individual tracks show some level of connectivity between the central and eastern Mongolian migration routes. For instance, sg208 (male adult) undertook a different spring migration route from that of most birds from central Mongolia, joining with birds caught at Hulun Lake (one of the largest freshwater lakes China) early in spring migration, but after arrival at Hulun Lake he continued onwards to arrive on the central Mongolia breeding grounds a week later. Three Swan Geese (sg211: male juvenile, sg142: male adult, sg96: female adult) from eastern Mongolia moved to the upper Kherlen River where they mixed with birds from central Mongolia, then continuing onwards together to stopover sites and wintering areas further south. One of these (sg047, a female adult), which moulted on Hulun Lake, spent the summer > 1,200 km away near Khanka Lake the following year.

The Coastal flyway was defined by three individuals, which contributed spring migration data from Jianghua Bay in South Korea to Udyl Lake. Unfortunately, we lack migration data from Jianghua Bay to the Minjiang Estuary, but since only relatively few Swan Geese winter in Korea (see below), we think it highly likely that larger numbers of staging birds continue to winter on the Minjiang Estuary. This population migrates along the lower Han River and Khanka Lake, with some continuing along Amur River to summer near Udyl Lake in Far East Russia (Fig. 3).

Population size and trends of wintering populations

The total wintering number of Swan Geese was estimated at 54,400 in East Asia in January 2020, based on counts of *c.* 54,000 birds along the Yangtze River, 368 in the Minjiang Estuary and 47 in South Korea (Table 3). Fewer than 10 Swan Geese have been counted annually at all sites monitored in Japan since 1970, with only three individuals counted in 2019, so we conclude that the species is no longer a regular wintering visitor to Japan (Supporting Materials Table S3).

The Inland population constitutes the largest population of Swan Geese in East Asia, but all indications are that the wintering numbers are decreasing. Although based on incomplete surveys, there were at least 73,000 Swan Geese counted in eastern China (the Yangtze River floodplain and Jiangsu Province) during winters 1987/88–1992/93, whereas better count coverage in winter 2004/05 resulted in an estimate of *c.* 78,000 birds. The current estimated wintering number is based on improved survey coverage conducted in January 2020 (Table 3, Fig. 4). Just taking the recent counts at face value, numbers wintering on the Yangtze River showed a significant decline from 65,000 to 52,000 between winters 2003/04–2019/20 ($F_{1,11}$ = 6.45, r^2 = 0.39, P = 0.03; Fig. 4) and declines here are likely to have been even greater if dated back to the 1990s.

The Coastal population continues to decline and is currently facing extinction. From 2000 to 2017, the wintering numbers of South Korea were fewer than 100 (Table 3, Fig. 4), compared to 2,456 in 1998/99, with 112 in 2017/18, and 43 in 2019/20. Based on survey data from 2003/04 to 2019/20, numbers of Swan Geese wintering in the Minjiang Estuary also declined significantly ($F_{1,15}$ = 10.44, r^2 = 0.42, P = 0.006; Fig. 4).

Key wintering sites in China and South Korea

Given the revised estimates of Swan Goose numbers in the two flyways, the 1% criterion for determining sites of international importance for the species is now 540 birds on the Inland flyway, and four birds on the Coastal flyway (Table 3). On this basis, four key wintering sites in the Yangtze River floodplain were identified from the counts recorded between 2015/16 and 2019/20, including two regularly-used sites: Poyang Lake, Shengjin Lake, and two occasional sites: Taibo Lake and Wang Lake (Fig. 5, Supporting Materials Table S4). Given the parlous state of the Coastal flyway, we consider that all sites used by these birds to be of significance to the remaining population, but especially the core wintering area on the Minjiang Estuary in Fujian Province. There are still five key wintering sites in South Korea, including the Han Estuary, Sapgyo Reservoir, Janghang Coast, Suncheon Bay and the Junam Reservoir (Fig. 5, Supporting Materials Table S4).

Changes in numbers of Swan Goose at key wintering sites in China

The number of key wintering sites of Swan Geese in China decreased from eight to four during 2004–2020. Eight key Swan Goose wintering sites in the Yangtze River floodplain have been monitored during the non-breeding period since 2004 and 2005,

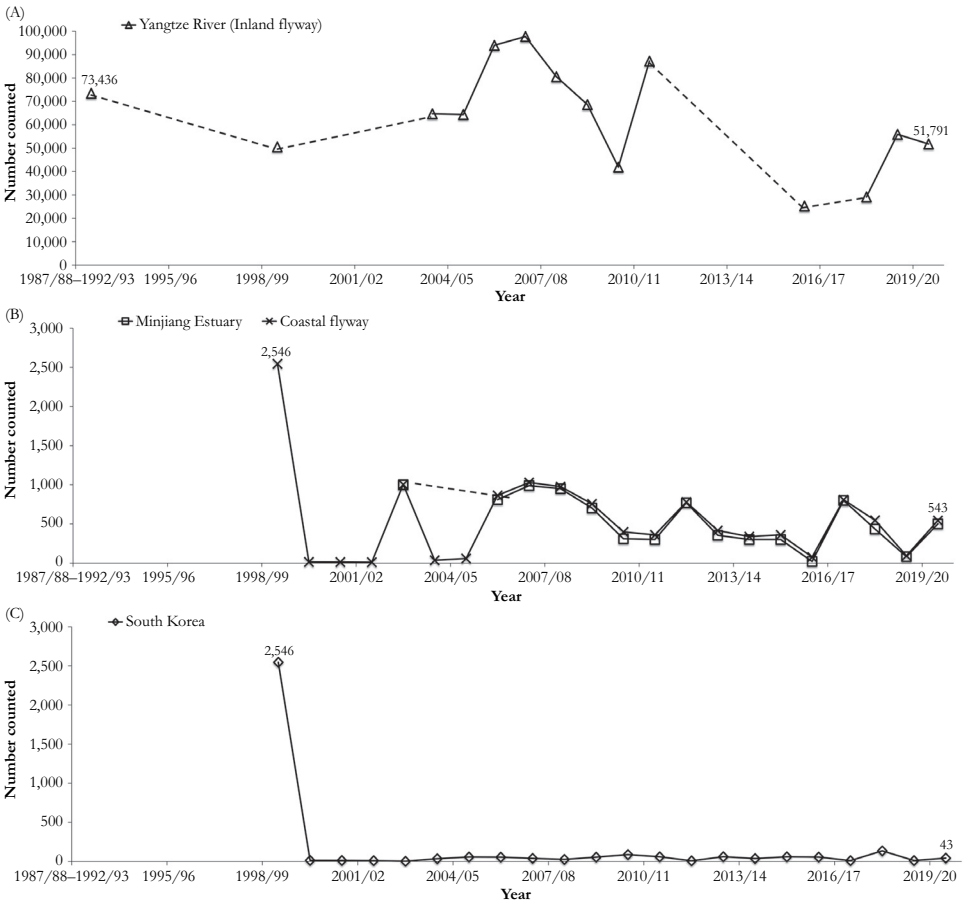

Figure 4. Abundance estimates and trends in wintering numbers of Swan Geese counted in the two flyways (Inland and Coastal) from 1987/1988–2019/20. Numbers in the Inland flyway (A) include counts from the Yangtze River floodplain in winters 1997/98–2010/11 from Jia *et al.* (2016); those for 2015/16–2019/20 were based on winter surveys (Supporting Materials Table S2). Counts of numbers in the Coastal flyway (B) were derived from winter surveys and the literature, including records from the Minjiang River estuary, Fujian Province, in winters 2002/03, 2005/06–2019/20 (B) and from South Korea (C) in winters 1999/2000–2019/20. As < 7 birds have been counted during coordinated winter waterbird counts in Japan since 1969/70 (see Supporting Materials Table S3), these numbers are not shown here. Dashed lines connect counts with interim missing count data in the intervening years.

including Poyang and Wang lakes in Jiangxi Province and the Anhui Lakes (Table 4). Of these, only three qualified as key wintering sites in 2019 and 2020 (Poyang Lake, Wang Lake and Shengjin Lake), mainly due to reductions in Swan Goose numbers in the Anhui Lakes after 2009 (at Fengsha, Caizi, Wuchang and Baidang Lakes, Fig. 6, Table 4).

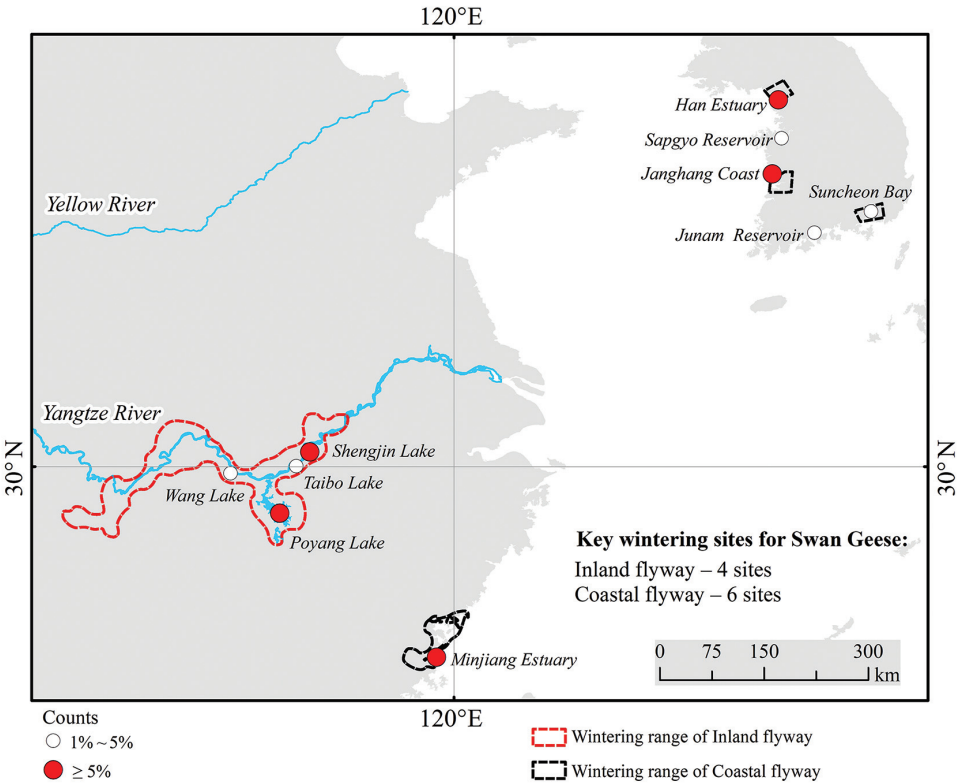

Figure 5. Key wintering sites for Swan Geese: four on the Inland flyway, in the Yangtze River floodplain (two important key sites; two occasional key sites) and six for geese in the Coastal flyway (three important key sites; three occasional key sites). Key wintering sites for the two flyways (1% criterion: 540 birds for Inland and four birds for Coastal geese) were determined from the total numbers recorded during 2015/16–2019/20 (see Supporting Materials Table S4 and *Methods* for details). Red and white circles = sites with ≥ 5% and ≥ 1% of the numbers of Swan Geese estimated for their flyways. Red and black dashed areas = wintering ranges of Inland and Coastal flyways, respectively.

Numbers of Swan Geese counted at Shengjin Lake declined significantly after 2006, although these have recovered to some extent in recent years. Wang and Taibo Lakes in Jiangxi Province, have qualified in recent years (Table 4). For birds using the Coastal flyway, Minjiang Estuary remains the key wintering site, with maximum wintering numbers during 2006 to 2020 fluctuating annually, but with a peak count of 1,200 in 2016 and a minimum of 300 in 2015.

Most wintering Swan Geese now increasingly concentrate at Poyang Lake (Table 4, Fig. 6). Numbers counted there have nearly doubled in recent winters, in comparison with counts recorded during the 2003/04–2004/05 winter surveys, which means the percentage of all Swan Geese

Table 4. Maximum number of Swan Geese counted at key wintering sites (n = 15) for two flyway populations during December–February in 2003/04–2019/20. For the Inland flyway population, five key sites were identified out of seven surveyed in winter 2003/04 (one with ≥ 1% and four with ≥ 5% of the total numbers counted), and four key sites were identified out of nine sites surveyed during the 2019/20 wintering survey (three with ≥ 1% and one with ≥ 5% of the total numbers counted). The geese mostly wintered at Poyang Lake and the Anhui Lakes until 15 years ago, but now winter at Poyang and Shengjin Lakes, and also occasionally at Wang Lake, whilst numbers wintering at the Anhui Lakes have declined. Swan Geese of the Coastal flyway population mostly wintered in Minjiang River estuary, with peak counts ranging from 300–1,200 birds over the last 15 years. Few Swan Geese winter in South Korea.

Winter	Inland flyway population								Coastal flyway population						
	Poyang Lake	Wang Lake	Taibo Lake	Shengjin Lake	Fengsha Lake	Caizi Lake	Wuchang Lake	Baidang Lake	Mingjiang Estuary	Han Estuary	Sapgyo Reservoir	Janghang Coast	Suncheon Bay	Junam Reservoir	Nakdong Estuary
2003/04	24,403	52	–	11,483	10,950	6,469	1,500	156	–	–	–	–	–	–	–
2004/05	22,313	1,260	–	24,211	4,947	7,002	22	870	–	–	–	–	–	–	–
2005/06	–	–	–	13,452	–	–	–	–	810	–	–	–	–	–	–
2006/07	–	–	–	8,361	–	–	–	–	989	–	–	–	–	–	–
2007/08	–	–	–	2,400	–	–	–	–	950	–	–	–	–	–	–
2008/09	–	–	–	1,953	–	–	–	–	702	–	–	–	–	–	–
2009/10	–	–	–	1,295	32	524	409	132	420	0	0	75	4	9	0
2010/11	–	–	–	596	0	72	8	3,800	800	0	0	47	2	2	9
2011/12	–	–	–	207	354	–	0	3,210	770	0	0	0	3	0	6
2012/13	–	–	–	266	0	–	310	43	850	0	0	44	10	7	0
2013/14	–	–	–	1	0	–	2	3,556	850	0	0	21	15	0	0
2014/15	7,524	–	–	49	0	5	2	11	300	0	0	57	1	2	0
2015/16	18,863	0	–	132	0	45	0	0	1,200	53	0	0	2	2	0
2016/17	38,796	–	–	261	11	0	0	14	800	2	5	0	0	2	0
2017/18	40,774	100	710	370	0	27	1	54	435	0	0	108	0	4	0
2018/19	40,489	55	39	14,477	0	202	42	0	330	4	0	0	0	7	0
2019/20	48,341	755	126	1,700	0	124	0	0	500	11	0	26	6	0	0

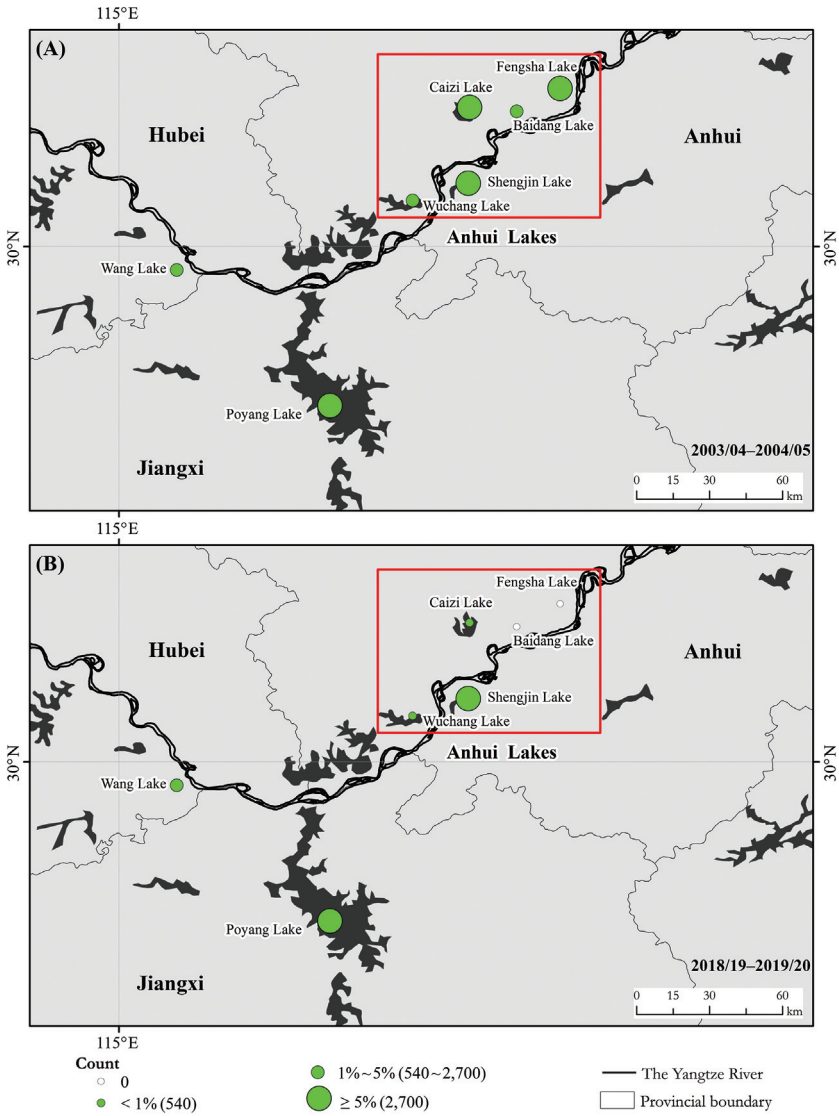

Figure 6. Map illustrating changes in the numbers and distribution of key wintering sites for Inland flyway Swan Geese in their core wintering area – the Yangtze River floodplain, China. Seven key sites (three with 1% and four with 5% of the total numbers estimated for the flyway) were identified in winters 2003/04 and 2004/05 (A). Three key sites (one 1% key site; two 5% key sites) were found among the seven sites surveyed in 2018/19 and 2019/20 (B). White circles = sites that were visited but no Swan Geese were present. The size of the green circles indicates numbers counted as a proportion of the total of numbers of Inland flyway geese counted in the Yangtze River floodplain that winter. Lakes within the red rectangle = the Anhui Lakes.

wintering at Poyang Lake has increased from 40%–50% during 2003/04–2004/05 to 70–90% during 2018/19–2019/20. The distribution of Swan Geese within Poyang Lake has also changed in recent years, with the majority using the centre of the site during 2018/19 and 2019/20, compared to a more widespread, peripheral distribution in 2004/05 (Fig. 7).

Discussion

Distribution range

Combining satellite tracking data, survey data and expert opinion, we have been able to identify, revise and update the entire summer and winter ranges of two flyways of Swan Geese – the Inland flyway and the Coastal flyway. For the Inland flyway, updated information and new migration data confirm that the core part of the Swan Goose summering range lies within Mongolia, adjacent parts of Russia, and northeast China, with a considerable contraction of the summering range in Russia and northeast China reported in BirdLife International and Handbook of the Birds of the World (2019). The reduction in the summer range in Russia has been linked to natural habitat loss and illegal hunting (Kear 2005; Poyarkov 2005). Extensive habitat loss caused by wetland reclamation and agricultural development, human disturbance and illegal hunting has also seriously reduced the summer range of this species in northeast China (Li 1996; Zhang *et al.* 2018). Khanka Lake provides an important location on both flyways, *e.g.* the summering area of Inland flyway Swan Geese as well as a staging area of Coastal flyway birds, and the disturbance from human activities and loss of wetlands in this area have also reduced the numbers of Swan Geese using the site (Feng *et al.* 2005). We have added to the summering range, the area around Xilin Gol in Inner Mongolia to Kangba Noel, which is known to hold summering geese based on survey data collected during the current study, not previously described on the distribution maps. Kangba Noel represents the extreme southeast edge of the breeding range, located in the northwest Hebei Province on the border with Inner Mongolia. This area lies on the southernmost edge of the Mongolia Plateau, and supports breeding Swan Geese due to its more stable hydrology and reduced human disturbance (Wu *et al.* 2017). Summer movements of GPS-tagged Swan Geese showed that the species concentrated in rivers and small lakes on the Mongolia steppe, although we lack survey coverage throughout this biogeographical region to confirm the precise breeding extent of the species. For birds using the Coastal flyway, the summer range is much reduced compared to historical times (Fox & Leafloor 2018), and all indications suggest numbers are decreasing (continuing earlier declines; Poyarkov 2005), thus requiring urgent and continuous monitoring of this isolated, small population. The key moulting sites of Swan Geese in Mongolia were also derived from the tracking data; eastern Mongolia and Inner Mongolia are vital for moulting Swan Geese, although more information based on satellite tracking research and field survey work is needed to supplement these findings.

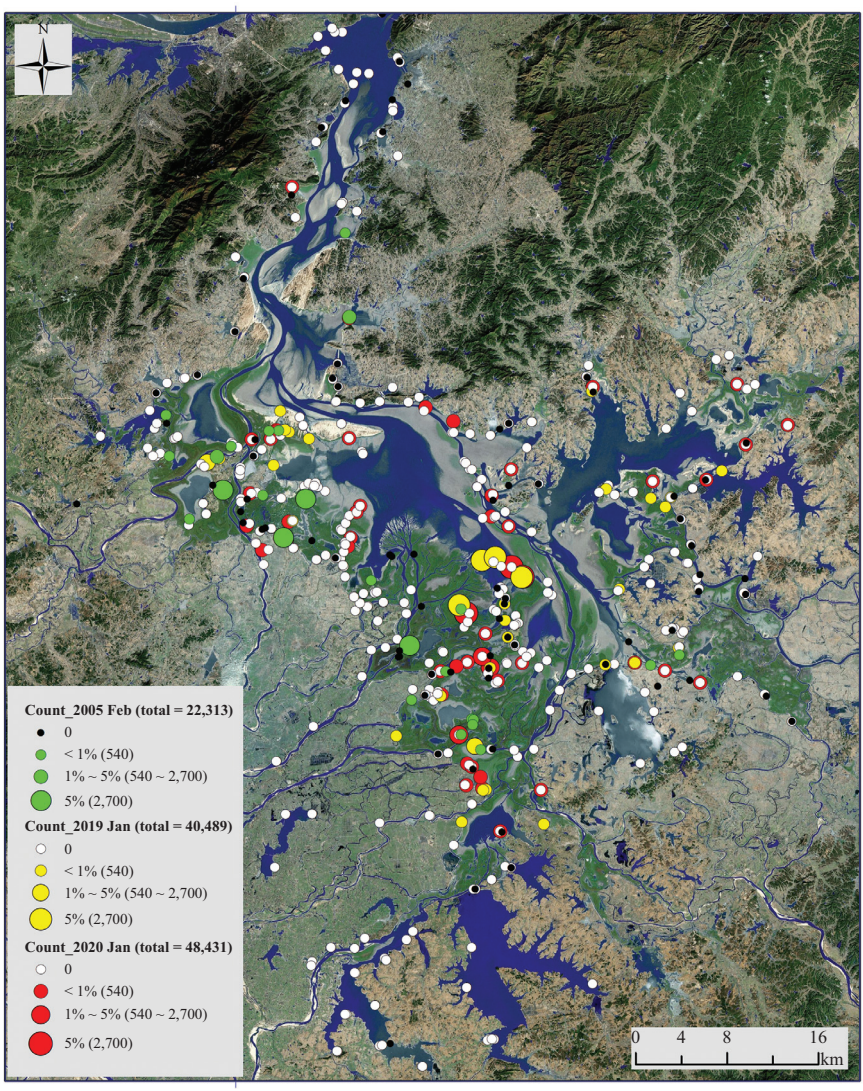

Figure 7. Survey points and changes in numbers of Swan Geese counted across Poyang Lake in winters 2004/05, 2018/19 and 2019/20. Total numbers at Poyang Lake accounted for 35% of Swan Geese on the Inland flyway in 2005, increasing to 72% and 94% in 2019 and 2020. Since the 2004/05 survey, additional survey points have been added, with new locations used by the geese identified by the tracking data. Consequently, numbers recorded have recently doubled. Whilst the species was once widespread and dispersed around the periphery of the lake (in 2004/05), large Swan Goose flocks (up to 2,700 birds) were more common in the centre of the lake in 2018/19 and 2019/20. Circle sizes = numbers counted as a proportion of the total individuals recorded for the Inland flyway along the Yangtze River that winter.

Currently, the global wintering range of Swan Geese is concentrated in the central and lower Yangtze River floodplain and the Minjiang River estuary in southeast China, with very few in South Korea, and effectively none wintering in Japan (where they occurred in the 1950s (Poyarkov 2005; Fox & Leafloor 2018)). This recent concentration of Inland flyway birds onto the Yangtze River seems to be due to wetland loss in coastal areas, which formerly held greater numbers (Cao *et al.* 2010), but more regular surveys of these coastal wetlands are required to confirm the situation.

Migration route

The abundance of new tracking data supports the case for identifying two distinct flyways of Swan Geese. The Inland flyway was determined from telemetry data from Swan Geese caught in major summering areas (western, central and eastern Mongolia, Hunlun Lake in Inner Mongolia of China) and at key wintering sites (Poyang Lake and the Anhui Lakes in the Yangtze River floodplain), so our inferences from these data are limited by our catch sites. The eastern Mongolian migration routes identified here were consistent with the results of Batbayar *et al.* (2013), while the sample size from other sites in eastern Mongolia also have been increased to confirm these patterns. It is clear that if Swan Goose pairing occurs on the wintering grounds (as seems likely), the increasing concentration of Inland flyway birds at a very few sites in the Yangtze River will not lead to structuring within the population. Hence, despite the clear migratory geographical separation of Swan Geese imposed by their summer provenance in the Inland flyway, winter panmixia would be expected to inhibit any differentiation of the gene pool. Future research will need to increase sample sizes from northeastern China and Khanka Lake, to determine the migration routes of these small groups of individuals that contribute to the eastern fringe of the Inland flyway. Some individuals of the Inland population showed unexpected elements to their migration routes, such as sg047 which moulted on Hulun Lake, but migrated to near Khanka Lake the following summer for breeding. Such long-distance moult migration would further contribute genetic mixing between birds of widely-spaced summering locations within the Inland flyway. In addition, sg226, which was originally caught in eastern Mongolia during the moulting period, undertook the shortest of spring migration routes, from the winter area of the Yangtze River floodplain to the south part of Kangba Noel in late April, although unfortunately we subsequently lost the signal from this device. Our lack of knowledge from this southernmost part of the summer range of the Swan Goose also requires further telemetry combined with field investigation to explain the importance of this area.

Available data suggests that birds using the Coastal flyway are extremely few in number and require considerable research and conservation investment. Although the migration routes of three individuals were consistent with the results of previous migration routes of ringed birds in Far East Russia (Poyarkov 2005; Choi *et al.* 2016a; Fox & Leafloor 2018), we lack firm connections between breeding, staging and

wintering areas. Unpublished results from another tracking study showed that one South Korean-caught individual, which summered in Far East Russia migrated to Fujian Province for wintering (Choi Chang Yong, unpubl. data). However, we require further evidence from tracking Swan Geese in this flyway to confirm the connections between Far East Russia, South Korea and the Minjiang Estuary, as well as the key staging sites and habitats used throughout the annual cycle. Given the lack of major spatial overlap throughout the annual cycles between the Inland and Coastal flyways based on current satellite tracking data, we would predict greater genetic variation between birds from these two flyways than within. Preliminary genetic investigation of the mitochondrial DNA, which found that the haplotypes in Far East Russian summering Swan Geese differ from those of the Inland population (Zhu Qin, unpubl. data), suggests that this may be the case.

Abundance and trends of wintering populations

We presented the most recent wintering numbers and updated the population trends of the two flyways of Swan Geese in recent years (2012–2020). From the systematic Yangtze River surveys undertaken in 2003/04, 2004/05, 2015/16, and 2017/18–2019/20, compared to the more limited counts in the 1990s, it would appear that numbers of birds using the Inland flyway have been declining for at least two decades. Declines may be more serious than we can account for, because the Yangtze River floodplain survey coverage in 2018/19 and 2019/20 was extended to sites identified from satellite tracking data, which included more intensive survey of the centre of Poyang Lake (Fig. 7). Hence, in general, we would argue that the count coverage if anything has increased over the period we have described a decline in the population as a whole. Regarding Swan Geese using the Coastal flyway, wintering numbers on the Minjiang River estuary have decreased, strongly suggesting a major decline in wintering numbers of Coastal birds, possibly due to the low annual survival rate (Choi *et al.* 2016a). In addition, wetland loss in coastal areas during recent years may also contribute to decreased wintering numbers on the Minjiang Estuary (Cao *et al.* 2010). It therefore remains a priority to improve the waterbird monitoring programme to cover wintering Swan Geese systematically, both in the Yangtze River floodplain and the coastal areas of South Korea and China in the immediate future, combined with ecological research and demographic monitoring of the population. This would enable us to understand better the population dynamics of this species and the pressures throughout the annual cycle.

Key wintering sites in China

Our study updated the list of key wintering sites for Swan Geese in China based on recent wintering survey data. Compared with the 1% criterion from Wetlands International (2020) for East Asia, the 1% criterion for this species derived from our study is slightly lower due to the decline in overall population size. Swan Geese of the Inland flyway concentrated at Poyang Lake and Shengjin Lake in recent winters, compared to a more widespread distribution in earlier years (Jia

et al. 2016). Key wintering sites for Swan Geese in the Yangtze River floodplain have changed significantly over the past decade, including loss of key sites in Anhui such as Fengsha, Wuchang, Caizi, Baidang Lakes, perhaps due to the disappearance of submerged plants, possibly linked to aquaculture and/or changes in water level management (Fox *et al.* 2011; Zhang *et al.* 2011). Wintering numbers of Swan Geese at Shengjin Lake decreased from 2003/04 to 2009/10, but have increased since 2018/19, a phenomenon which is likely linked to the sympathetic nature of conservation management measures implemented by the Nature Reserve authorities at the site in recent years, such as returning farmland to lake wetlands and banning aquaculture. The major importance of Poyang Lake (now supporting 90% of all Swan Geese) means that its sympathetic management is paramount to the global population of this species. Changes in water levels have been shown to affect the feeding habitat of Swan Geese at that site (Aharon-Rotman *et al.* 2017) and proposed dams are predicted to have an adverse effect on its hydrology in the future. For this reason, it is necessary to maintain long-term monitoring of Swan Geese at Poyang Lake, and undertake research to provide scientific advice for optimising habitat management in the face of hydrological change.

Along the Coastal flyway, the development, degradation and destruction of coastal wetlands in China in recent years have undoubtedly led to major reductions in the winter carrying capacity and ultimately the numbers of Swan Geese in the Minjiang Estuary. Given the lack of research on this key site, future plans should prioritise the tracking of the species throughout the flyway, but particularly within Korean staging areas and the Minjiang Estuary complex to establish the major feeding areas, the nature of their diet and the areas used as safe roost sites, to determine the main areas requiring protection.

Conservation management

To understand fully the distribution, abundance, important habitats and life cycle events of the globally vulnerable Swan Goose, it is necessary to combine research and conservation efforts in Russia, Mongolia, China and South Korea, to establish a long-term scientifically-based monitoring system. Results should then inform sympathetic management of the habitats that these birds exploit throughout their migratory range. Habitats used by the geese are under serious threat from a range of factors at different stages of the annual cycle, so research on site use by the species remains an urgent priority, to provide a scientific basis for the protection of Swan Geese through best management of their environment. Birds using the Coastal flyway are at particular risk of extinction, and a combination of field surveys and satellite-tracking studies are needed to provide a better assessment of the population status. As breeding and moulting periods are critical for Swan Geese, it is essential that the logistical efforts of all countries be combined in order to monitor key breeding and moulting areas. Finally, since the vast majority of all Swan Geese are concentrated in Poyang Lake, we urge for more research at this site for a better understanding of habitat use at the

lake which could provide insights to support more sympathetic management at other sites, to restore numbers where these have declined in recent years.

Acknowledgements

We gratefully acknowledge the key contributions to the fieldwork from the capture teams in Mongolia (WSCC) and in China (Hulun Lake and Poyang Lake NNR). We would like to thank Xianghuang Li for capture work, and Yanbo Xie and Xin Wang for guidance and advice during this study. We greatly appreciate help from Dali Gao during the Yangtze survey. The authors acknowledge funding from the CAS-TWAS President Ph.D. Fellowship Program. The study was also supported by the National Key Research and Development Programme of China (Grant Nos. 2017YFC0505800), the National Natural Science Foundation of China (Grants No. 31670424, 31870369), the Chinese Academy of Sciences Key Strategic Programme, Water Ecological Security Assessment, the Major Research Strategy for Middle and Lower Yangtze River (Grant No. ZDRW-ZS-2017-3-3), and the China Biodiversity Observation Networks (Sino BON). The funders have had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. The Animal Ethics Committee, Research for Eco-Environmental Sciences, Chinese Academy of Sciences fully approved this study. Approval for bird capture and transmitter deployment was obtained from Mongolia (Ministry of Nature, Environmental and Tourism (MNET) of Mongolia; Permission No. 06/2008, 06/2862, No. 11120), China (Jiangxi Forestry Bureau; Ref. No. Ganlinban 201571), and South Korea, as well as from the Animal Ethics Committee at the Research for Eco-environmental Sciences, Chinese Academy of Sciences. We also thank two referees for their constructive suggestions for improving the paper.

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Photograph: Group of Swan Geese on grassland in Inner Mongolia, China, by Staffan Widstrand/Wild Wonders of China/naturepl.com.