Rapid decline of the geographically restricted and globally threatened Eastern Palearctic Lesser White-fronted Goose *Anser erythropus*

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Abstract

The Lesser White-fronted Goose *Anser erythropus*, which breeds across northern Eurasia from Norway to Chukotka, is globally threatened and is currently classified as Vulnerable by the International Union for Conservation of Nature. The Eastern Palearctic population of the species was thought to breed in arctic Russia, from east of the Taimyr Peninsula to Chukotka, and to winter in East Asia, but its precise status, abundance, breeding and wintering ranges, and migration routes were largely unknown, reducing the effectiveness of conservation efforts. In this paper, we combined results from satellite tracking, field surveys, a literature review and expert knowledge, to present an updated overview of the winter distribution and abundance of Lesser White-fronted Geese in the Eastern Palearctic, highlighting their migration corridors, habitat use and the conservation status of the key sites used throughout the annual cycle. Improved count coverage puts the Eastern Palearctic Lesser White-fronted Geese population at *c.* 6,800 birds in 2020, which represents a rapid and worrying decline since the estimate of 16,000 in 2015, as it suggests at least a halving of numbers in just five years. East Dongting Lake (Hunan Province) in China is the most important wintering site for the species in East Asia, followed by Poyang Lake (Jiangxi Province) and Caizi Lake (Anhui Province), with one key wintering site in Miyagi County in Japan. Satellite tracking showed that eight individuals captured during summer on the Rauchua River, Chukotka, Russia wintered in the middle and lower reaches of the Yangtze River floodplain in China. Their migration speed was slower in spring than in autumn, mainly because of longer stopover duration at staging sites in spring. The tracked geese mainly used cultivated land on migration stopovers (52% in spring; 45% in autumn), tundra habitat in summer (63%), and wetlands (66%) in winter. Overall, 87% of the GPS fixes were in protected areas during the winter, far greater than in spring (37%), autumn (28%) and summer (7%). We urge more tracking of birds of differing wintering and breeding provenance to provide a fuller understanding of the migration routes, staging sites and breeding areas used by the geese, including for the birds wintering in Japan. The most urgent requirement is to enhance effective conservation and long-term monitoring of Lesser White-fronted Geese across sites within China, and particularly to improve our understanding of the management actions needed to maintain the species. Collaboration between East Asian countries also is essential, to coordinate monitoring and to formulate effective protection measures for safeguarding this population in the future.

Key words: abundance, key sites, migration routes, population trends, telemetry tracking.

The Lesser White-fronted Goose *Anser erythropus* is a globally threatened species, designated as Vulnerable by the International Union for Conservation of Nature (BirdLife International 2018). Historically and for convenience, the species has been divided into three populations worldwide: the Fennoscandian, Western Main and Eastern Palearctic populations (Fox & Leafloor 2018). The Eastern Palearctic population of the Lesser White-fronted Goose breeds from east of the Taimyr Peninsula to Chukotka (Morozov & Syroechkovskiy 2002, 2005; Fox & Leafloor 2018). These birds winter predominantly in the middle and lower reaches of the Yangtze River in China, although in former times Lesser White-fronted Geese were highly concentrated at

East Dongting Lake (Wang *et al.* 2012), with much smaller numbers in South Korea and Japan (Fox & Leafloor 2018). In the 1980s, the number of Lesser White-fronted Geese wintering in China was estimated at 65,000 individuals, which were widely distributed in Anhui, Hubei, Jiangsu, Jiangxi, Hunan and other provinces (Wang *et al.* 2012; Jia *et al.* 2016). Since that time, the species has suffered a sharp decline in numbers, and has become concentrated in Dongting Lake in Hunan Province (Wang *et al.* 2012; Jia *et al.* 2016), due to habitat loss and degradation in the Yangtze River floodplain, hunting, and the specialised feeding ecology of the species (Wang *et al.* 2013). A more recent estimate has put the Eastern Palearctic population at *c.* 16,000 individuals (Fox & Leafloor 2018). Telemetry studies found that individuals from the Eastern Palearctic population migrated from Dongting Lake in China to the Russian taiga and arctic tundra regions in spring, with the main staging area for these birds being in the eastern part of China (Lei *et al.* 2019a). Stopover sites were also located in the lower reaches of the Amur River in Russia and along the Sea of Okhotsk coast (Fox & Leafloor 2018), but generally the migration routes taken in autumn are poorly known. In very recent years, numbers of Lesser White-fronted Geese wintering in Japan have increased, with migration observed through the Sarobetsu wetland in northern Hokkaido, but their precise migration routes are also unknown (Ikawa 2010).

Illegal hunting, habitat destruction, habitat loss and human disturbance still pose severe challenges to conserving birds throughout the world. In response, the establishment of networks of protected areas to combat these threats and to protect species remains one of our first lines of defence for conserving migratory bird populations throughout their annual cycle (Kirby *et al.* 2008). However, designation of cohesive networks of protected areas needs a scientific basis to ensure the most effective implementation of such conservation interventions. Assessing use of the protected wetland network by waterfowl throughout their entire annual cycle, in relation to the perceived needs for safeguarding their sites, is the ideal approach to testing the effectiveness of existing protected area networks (Beatty *et al.* 2014). Knowledge of the location of stopover/wintering/summering sites, their linkages, and their relative importance to the population is crucial for the effective conservation of the Eastern Palearctic Lesser White-fronted Goose population and for mitigating against the effects of land use and climate change, yet such knowledge about their use of migration routes and locations is still lacking (Wang *et al.* 2018a).

Many East Asian waterfowl species have declined rapidly in the last 10–20 years and critical knowledge gaps concerning their migration ecology remain (Si *et al.* 2018). Recent advances in genetics, isotope analysis and satellite telemetry have greatly improved our understanding of migration patterns of many species (Webster *et al.* 2002; De La Cruz *et al.* 2009; Bridge *et al.* 2015). For example, until recently, almost nothing was known about Far East Asian migration routes, phenology, and the links between the summer and winter locations of common geese and duck species, but with the use of satellite telemetry and stable isotope analysis of feathers, our understanding of their migration ecology, connectivity and range changes has vastly improved (Yu *et al.* 2017; Wang *et al.* 2018a,b; Zhu *et al.* 2020).

Nevertheless, we lack a comprehensive understanding of the migration routes and abundance of the Eastern Palearctic population of the Lesser White-fronted Goose, as well as an assessment of the extent of site protection at their main summering, moulting, stopover and wintering sites, knowledge required for the effective conservation of this declining population. The aim of this study therefore was to improve our understanding of Lesser White-fronted Goose distribution, migration routes, stopovers and habitat use, and to assess the conservation status of key areas used by the Eastern Palearctic population. To do so, we combined results from field surveys, with expert knowledge and GPS tracking data, to generate updated population estimates, assess historical trends, and identify key wintering sites in China, South Korea and Japan along with locations used by the geese elsewhere along the flyway. The spring and autumn migration parameters were also described and compared, to provide baseline information on the movements of the species in East Asia.

Methods

Migration data

In summer 2018, 10 adult Lesser White-fronted Geese of unknown sex were captured along the Rauchua River (68°48'N, 167°38'E) in the Russian arctic (Solovyeva & Vartanyan 2011). Flightless birds were rounded up during their annual summer moult and manoeuvred by boat from the water onto river banks, where they were captured by hand. These individuals were all fitted with backpack solar-powered GPS transmitters (Ornitela, Lithuania, 25 g) secured with Teflon ribbon (Bally Ribbon Mills, < 5 g) before release (see Supporting Materials Table S1). Additionally, in 2017 a single adult goose (sex unknown) was captured on its wintering grounds at Chenyao Lake (30°54'N, 117°40'E) one of the Anhui lakes in the Yangtze River floodplain, China. This bird was dazzled using a powerful lamp at night and taken by hand-net into a boat where it was tagged and released with a 35 g solar-powered collar mounted GPS transmitter (Druid Technology, China). Both types of devices fitted to the geese recorded positions (with 19–128 regular GPS positions per day, contingent upon power supply) and transmitted these data via GSM mobile phone networks (Supporting Materials Table S1). Only nine individuals with devices that provided full data throughout at least one complete spring or autumn migration were used to identify the migration routes and parameters. First-day movement data after birds were captured and tracked, and last-day data before birds died or lost contact, were excluded from the analyses because of the risk of abnormal behaviour at these times.

We searched for and collected migration information relating to Lesser White-fronted Geese on the Web of Science using the terms: (geolocat* OR GPS OR Argos OR PTT OR CTT OR (satellite* AND (track* OR transmitter* OR telemetr*))) AND ("lesser white-fronted goose" OR "lesser white-fronted geese" OR "anser erythropus"), and on Google Scholar using the terms: ("lesser white-fronted goose" OR "anser erythropus") AND (track OR migration) AND (GPS OR ARGOS OR geolocator); date to 31 October 2020. The results published by Lei *et al.* (2019a) were found after this process, and so the migration routes taken by tagged Lesser White-fronted Geese caught in the Yangtze River in that study were digitised and are also presented here.

Distribution of the Eastern Palearctic population

An overview of the distribution of the Eastern Palearctic Lesser White-fronted Goose population was initially derived from the distribution map of BirdLife International and Handbook of the Birds of the World (2019). This was revised in line with counts recorded for the species in winter (see *Abundance estimates and trends in East Asia* section in *Methods*), and by links established between the wintering and summering areas derived from satellite-tracking data (see *Migration data* section in *Methods*) and expert knowledge. All these sources of knowledge were combined to produce a revised and updated map of the ranges and migration routes of Lesser White-fronted Geese in East Asia. All maps were managed and illustrated in ArcGIS 10.2 (ESRI 2013).

In October 2019, the "*2nd International Symposium on Developing Effective Coordinated Monitoring of East Asian Waterbirds in the 21st Century*" was held in Beijing, China. During the symposium, 10 experts from six countries in the East-Asian Continental & West Pacific flyway discussed and contributed further to the delineation of the migration routes and distribution of the Eastern Palearctic Lesser White-fronted Goose, as well as providing literature sources and unpublished data to support the modifications presented here (Supporting Materials Table S2).

Abundance estimates and trends in East Asia

Estimates of the numbers of Lesser White-fronted Geese wintering in China prior to 2012 were obtained from Jia *et al.* (2016). Synchronous Yangtze waterbird surveys during mid-January to early February in winters 2003/04, 2004/05, 2015/16, 2017/18, 2018/19 and 2019/20 are considered to have covered the majority of wintering Lesser White-fronted Geese in China at that time (Cao *et al.* 2010; Jia *et al.* 2016). The survey methods used in winters 2018/19 and 2019/20 were consistent with the survey methods for wintering waterbirds in the middle and lower reaches of the Yangtze River floodplain in 2003/04 and 2004/05 (Barter *et al.* 2004, 2006), although some new survey sites were added based on results of the satellite tracking data from Lesser White-fronted Geese. Waterbird count survey coverage (count vantage points and areas covered) were mapped on Google Earth images, and then converted into a Shapefile in ArcGIS 10.2 (ESRI 2013). The tracking fixes from January 2020, generated from the three tagged individuals which provided data in that month, were used to establish the proportion of positions which would have fallen within the survey coverage area in winter 2019/20, to estimate the potential survey coverage of the wintering population.

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

In Japan, annual mid-winter (*c.* 15 January) surveys of waterfowl (including Lesser White-fronted Geese) have been conducted since 1970 by the Ministry of the Environment with the assistance of prefectural governments. This nationwide survey covers all of the principal sites for swan, goose and duck species throughout the country during the season (Ministry of the Environment 2019). Annual winter (November–March) surveys of Lesser White-fronted Geese have also been conducted since 2013 by Hirofumi Hala and Toshio Ikeuchi. This expert survey covers all of its major known wintering and staging sites throughout Japan.

Simple linear regressions were applied to detect trends in abundance in each country, with log10(x + 1)-transformed country estimate as the dependent and year as the independent variable. Initial exploration of linear regression residuals of temporal trends in the China count data, fitted using the nlme package (Pinheiro *et al.* 2020), showed only minor evidence of statistically significant residual temporal autocorrelation at time lag 6, but for all other time lags $P > 0.05$ (n.s.). Given the lack of serial residual autocorrelation, no autocorrelation structure was included in subsequent linear regression analyses.

Key wintering sites of Lesser White-fronted Geese in East Asia

Key wintering sites for Lesser White-fronted Geese in China and Japan were determined from survey data recorded during 2015/16–2019/20, and were classed as such if they supported ≥ 1% of the new Eastern Palearctic population estimates at least once during this period. Although the number of years of data is relatively short for China, this measure is based on Criterion 6 of the Ramsar Convention, which states that a wetland should be considered internationally important if it regularly supports 1% of the individuals in a biogeographic population of one species or subspecies of waterbird (Ramsar Convention Secretariat 2010; https://www.ramsar.org/about-the-convention-on-wetlands-0).

Changes in the numbers and distribution of the Lesser White-fronted Geese at their main wintering sites in Chinese wintering sites during the past two decades were investigated by comparing annual maximum counts at key sites from winters 2003/04–2019/20. In addition to the survey data mentioned earlier in the *Methods*, surveys of key sites (Dongting Lake, Shengjin Lake and Anhui Lakes) along the Yangtze River floodplain in the non-breeding period of 2005/2006–2014/2015 were also included.

Migration parameters

Wintering/summering/stopover sites were identified via their use by telemetry tagged Lesser White-fronted Geese, using the methods of Wang *et al.* (2018b) to segment movement tracks and define stopover sites as locations where a bird did not move > 30 km over a 48 h period (Kölzsch *et al.* 2016). We defined moult migration as a series of continuous displacements of individuals from the last site within the (potential) breeding area towards a moulting site in late summer. Moulting area was defined as an area where tagged individuals stayed for > 21 days within a radius of 30 km within the period from 1 June–1 September (Aarvak & Øien 2003). Autumn migration was taken as starting from the first position after tagged individuals departed from the summering grounds and terminating with the first of a series of positions received from the wintering grounds. Likewise, spring migration was defined on similar criteria for the return to the breeding areas. Migration duration was calculated as the time that the bird took to travel (including stopovers) between the summering site and first wintering site (autumn migration), or between the last wintering and the first summering site (spring migration). Sites where individuals remained for more than 2 days were defined as stopover sites (Kölzsch *et al.* 2016) and the number of stopovers during a migration episode was calculated accordingly. Stopover duration was the sum of days spent at all stopover sites during each migration season. Thus, the days spent travelling (total travel days) was calculated as total migration duration minus stopover duration. A "migration leg" was defined as the journey that connected successive wintering, stopover or summering sites, totalled to provide the number of migration legs involved in each one-way (spring or autumn) migration. Migration distance was defined as the cumulative travel distance between wintering and summering sites (excluding movement within stopover/wintering/summering sites), and average step length was calculated as the migration distance divided by the number of migration legs during each migration. The average migration speed was then calculated as the migration distance divided by migration duration, and the average travel speed was calculated by dividing migration distance by total travel days.

The mean and variance of migration parameters in spring and autumn were calculated. Linear mixed effects models were used to compare the effects of season (*i.e.* spring and autumn) on nine migration parameters: migration duration, migration distance, migration speed, travel days, travel speed, number of migration legs, number of stopover sites, stopover duration, and step length, using these measures as fixed factors, with "Logger" and "Year" as random variables. Models were fitted using the nlme package (Pinheiro *et al.* 2020) in Program R. Model selection used the Akaike's information criterion corrected for small sample sizes (AICc). Candidate models with/without "season" were compared using AICc values, and the one with the lowest AICc value and where the difference was > 2 was considered the better model. If "season" was included in the better model, we determined that the corresponding migration parameter was significantly different between spring and autumn migrations. Among all combinations, models were selected using the "dredge" function in the R package "MuMIn" (Barton 2020). All estimates presented in tables and text are based on these estimated means (± s.e.) unless otherwise stated.

Land use and conservation status at stopover sites

In order to describe the types of habitat where tagged Lesser White-fronted Geese spent time, and the degree to which they remained within protected areas, we overlapped tracking locations with movement speed < 2 m/s (Wang *et al.* 2018a) at stopover/wintering/summering sites on land cover and protected area boundaries in ArcGIS 10.2 (ESRI 2013). Land cover types determined in 2017 were used, with a resolution of 10m x 10m created by the Ministry of Education Key Laboratory for Earth System Modelling, Department of Earth System Science, Tsinghua University, Beijing (Gong *et al.* 2019). The dataset is based upon ten defined land cover classification types, namely: bare land (*i.e.* uniform bare rock or other substrate), cultivated land, forest, grassland, artificial surface (*i.e.* built landscapes), shrubland, permanent snow/ice, tundra, water bodies and wetland. Seasonal wetlands might be misidentified as bare land due to the mismatch between the dates of land cover sampling (when bare mud) and the bird use (when potentially covered in shallow water or vegetation), and thus we reclassified bare land pixels based on Google Earth or Landsat images at the proximate date of bird use, using the same criteria as the original land cover dataset. Since Lesser White-fronted Geese rarely occur in closed canopy woodland, forest pixels were also visually reclassified from Google Earth and Landsat images, to control for misclassification in the original classification. These reclassified land use results were used and presented in this study. The boundaries for protected areas in Russia were extracted from the world database on protected areas (UNEP-WCMC 2017), and the boundaries of 471 national nature reserves in China were obtained from the Resource and Environment Data Cloud Platform (http://www.resdc.cn/).

The home range of tracked Lesser White-fronted Goose during different stages (wintering, summering and stopover sites) were calculated as a 0–95% utilization distribution (UD) using the fixed Kernel Density Estimation (KDE) method (Seaman & Powell 1996). KDE was calculated using the package "adehabitat" (Calenge 2006) in R 3.6 (R Core Team 2019) and mapped in ArcGIS 10.2 software (ESRI 2013).

Results

Distribution and migration range

Satellite tracking data, survey data and expert knowledge among the authorship of this article were integrated to summarise our understanding of the distribution and migration routes of the Lesser White-fronted Goose in East Asia. From accumulated expert opinion and the results of the telemetry studies, we can confirm that the approximate summer range of the Eastern Palearctic population in Russia extends from the Anabar River (73°69'N, 113°27'E) in the west across to the Anadyr River in the east (64°37'N, 178°44'E). However, because of the bias introduced from our restricted capture sites on the breeding areas, we cannot say very much about the breeding distribution and migratory range of this population. The results from a tracking study of Lesser White-fronted Geese marked on the wintering grounds (Lei *et al.* 2019a) was incomplete, as data were not obtained from spring migration routes all the way to the ultimate breeding areas, which are thought to be in the Russian taiga biome. However, these tracks show birds dispersing in diverse directions towards the inferred breeding area (arctic Russia) described by BirdLife International and Handbook of the Birds of the World (2019). For these reasons, we are not currently able to improve on the summer distribution maps for this species in the region (Fig. 1). In contrast, there is much to modify with regard to the wintering areas, especially in China, and as a result of the relatively few individuals that were wintering in Japan and irregularly in South Korea. The revised wintering areas in China were concentrated in the middle and lower reaches of the Yangtze River floodplain, while formerly occupied areas in Fujian, Guangxi, Guangdong, Hong Kong, Macao, Shenzhen have been deleted in the absence of recent records there (Fig. 1).

One should be very careful about concluding too much from inadequate data, but based on the available satellite tracking data, the Lesser White-fronted Goose in East Asia can probably be constituted as one flyway, *i.e.* the East-Asian Continental & West Pacific flyway (Fig. 1). This is based on the complete migrations of nine individuals (including 13 autumn migration routes and 6 spring migration routes) presented here, together with data from Lei *et al.* (2019a) and expert knowledge (Fig. 1). The results showed that individuals of this flyway, which summered on the arctic tundra of eastern Russia from central Yakutia to Chukotka, migrated along the Kolyma River, the Amur River and across the Sanjiang Plain (in northeast China) to winter at Dongting Lake, Poyang Lake and Shengjin Lake in the middle and lower reaches of the Yangtze River in China. The truncated migration routes extracted from Lei *et al.* (2019a) showed that the Lesser White-fronted Geese which wintered in the Yangtze River floodplain dispersed across the middle part of the extensive taiga zone during spring migration.

Abundance estimates and trends in East Asia

From 1969/70–2019/20, the trends in the wintering abundance of Lesser White-fronted Geese differed between China, Japan and Korea (Fig. 2, Supporting Materials Table S3). In China, the number of wintering Lesser White-fronted Geese decreased ($F_{1,13}$ = 39.667, r^2 = 0.768, $P < 0.001$) from 64,494 in the last century to 4,020 in 2019/20 (Fig. 2A). The number in South Korea has been consistently at < 10 individuals without a significant trend ($F_{1,19}$ = 0.427, r^2 = 0.023, P = 0.529, n.s.) from 1998/99–2017/18 (Fig. 2B). Numbers of Lesser White-fronted Geese have gradually increased from zero in the 1970s to 307 in 2019/20 in Japan ($F_{1,48}$ = 7.119, r^2 = 0.132, P = 0.012, Fig. 2C). The coordinated counts presented in this synthesis, including the possibility of birds

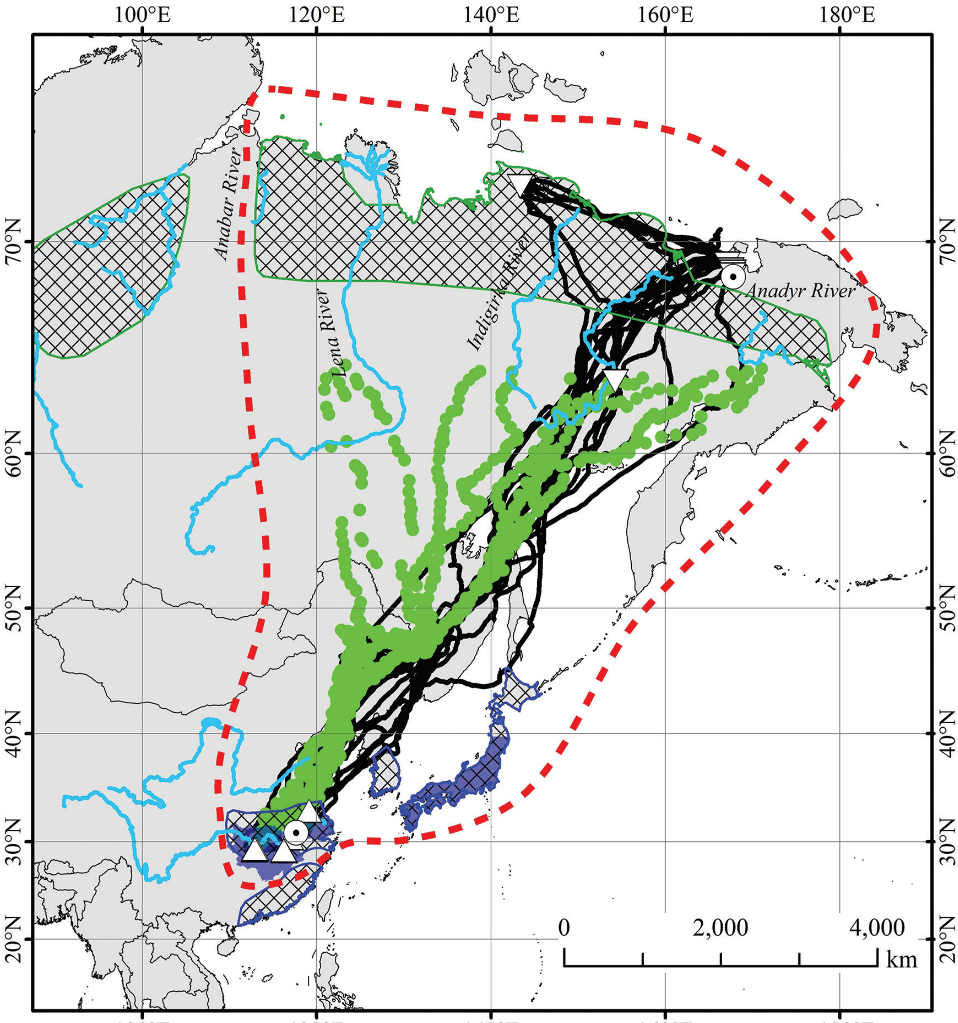

Figure 1. Revised distribution map and the full geographical East-Asian Continental & West Pacific flyway of the Lesser White-fronted Goose (red dashed line, birds summered in eastern Russia, wintered in China and Japan) based on migration routes of tracked individuals caught in China in winter (black solid lines; *n* = 9; green dots extracted from Lei *et al.* 2019a). The revised winter range (dark blue shading, mainly in central and eastern China and Japan) was modified from BirdLife International and Handbook of the Birds of the World (2019), on the basis of tracking data, field surveys data and expert knowledge (see *Methods* for details). Black grids = summer (edged green) and winter (edged blue) distributions from BirdLife International and Handbook of the Birds of the World (2019); circles with black dots = catch sites; inverted and regular triangles = summering and wintering areas used by tracked individual(s), respectively.

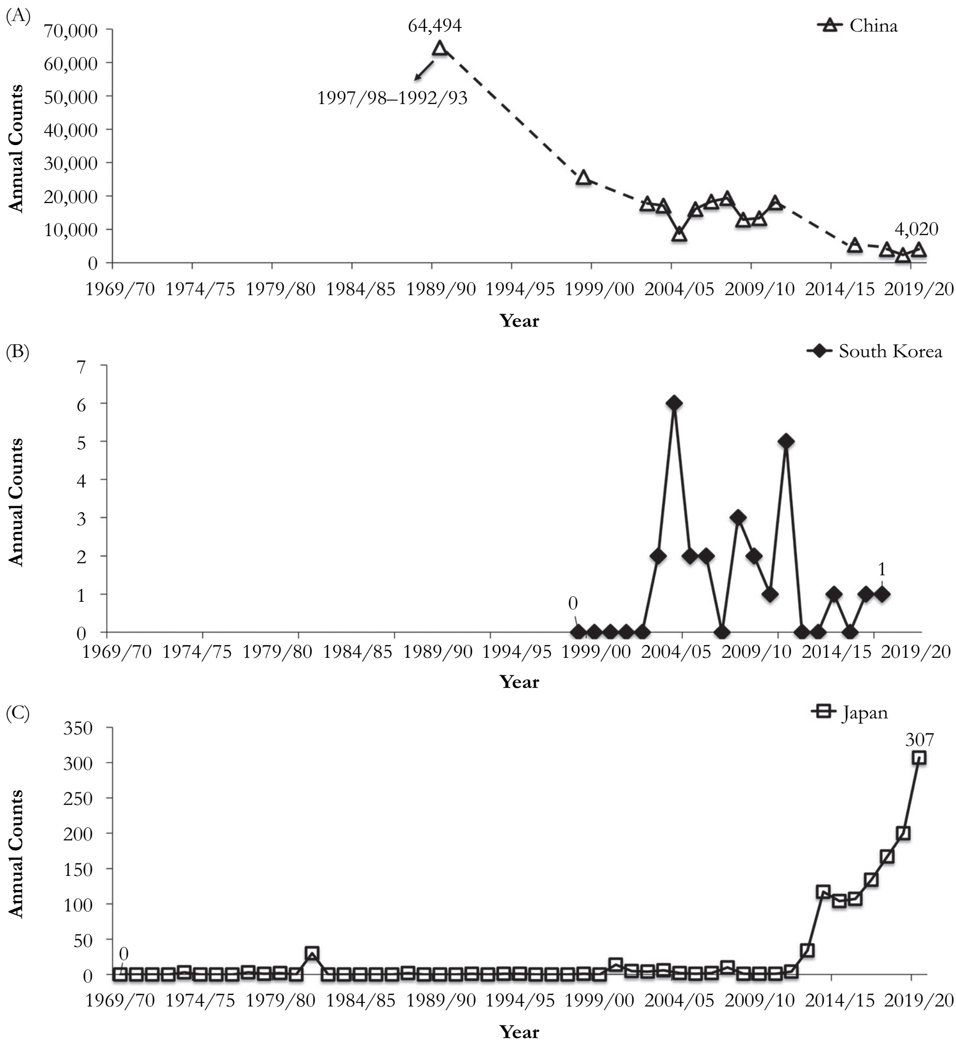

Figure 2. Numbers of Lesser White-fronted Geese counted in (A) China, (B) South Korea and (C) Japan in winters 1969/70–2019/20. Totals for Japan and South Korea are from winter surveys in 1969/70–2019/20 and 1998/99–2017/18, respectively. Chinese totals for winters 1987/88–2010/11 are from Jia *et al.* (2016); those for 2011/12–2019/20 are from winter survey data. Count totals are given for the earliest and most recent winters for which survey data are available in each country (also shown in full in Supporting Materials Table S3). Dashed lines indicate missing counts in intervening years.

missed during recent surveys, indicates that the Eastern Palearctic Lesser White-fronted Goose population numbered 6,800 birds in 2020, with 200 in Japan and 6,600 in China (average over the past five years divided by survey coverage; Table 1, Supporting Materials Table S3), generating a 1% threshold of 68 individuals for determining wetlands of international importance for the species (Table 1).

Key wintering sites of Lesser White-fronted Geese in East Asia

In China, three key (internationally important) wintering sites for Lesser White-fronted Geese were identified from the count data: East Dongting Lake (112°55'N, 29°20'E), Poyang Lake (116°15'N, 29°3'E) and Caizi Lake (117°7'N, 30°48'E), all within the Yangtze River floodplain (Fig. 3, Tables 2 & 3). One key wintering site for the species was identified in Japan, the Minamikacho (141°9'N, 38°40'E; Fig. 3, Table 2).

The number of Lesser White-fronted Geese counted at the four Chinese lakes identified as being of key importance changed after 2008/09 (Table 2). From 2003/04–2019/20, the numbers of Lesser White-fronted Geese counted in winter at East Dongting Lake have declined, although three new sites qualified during this period (Poyang Lake, Shengjin Lake and Caizi Lake, Table 2). In 2003/04, a total of 16,923 birds were counted in East Dongting Lake compared to 3,735 individuals in 2019/20, despite the fact that in recent years, the number of survey sites had gradually increased and covered more areas (Fig. 4). The overall trend suggests that birds have shifted from East Dongting Lake (where numbers have fallen dramatically) to sites in the lower reaches of the Yangtze River (Fig. 5). Although Poyang Lake (Jiangxi Province) has been one of the main

Table 1. Recent changes in abundance estimates and the current 1% level used to identify important sites for Lesser White-fronted Geese in East Asia.

Timing of population estimate	China	Japan	South Korea	Eastern Palearctic population
Population estimates in 2005	21,000[a]	2[b]	6[c]	–
Population estimates in 2011	18,080[d]	1[b]	1[c]	–
New population estimates	6,600[e]	190[f]	0[c]	6,800
New 1% criterion[g]	–	–	–	68

Sources: [a]Cao *et al.* (2008); [b]Ministry of the Environment of Japan unpubl. data, from annual nationwide surveys conducted in January 1996–2012 (raw count data in Supporting Materials Table S3); [c]Ministry of the Environment of South Korea unpubl. data, from the census of wintering birds conducted annually at 120 sites across South Korea, for January 1999–2018; [d]Jia *et al.* (2016); [e]mean of the peak numbers counted in China during winters 2015/16, 2017/18, 2018/19 and 2019/20; [f]mean of the numbers counted in each of the Japanese surveys during winters 2015/16–2019/20; [g]new population estimate, based on wintering abundance in China and Japan.

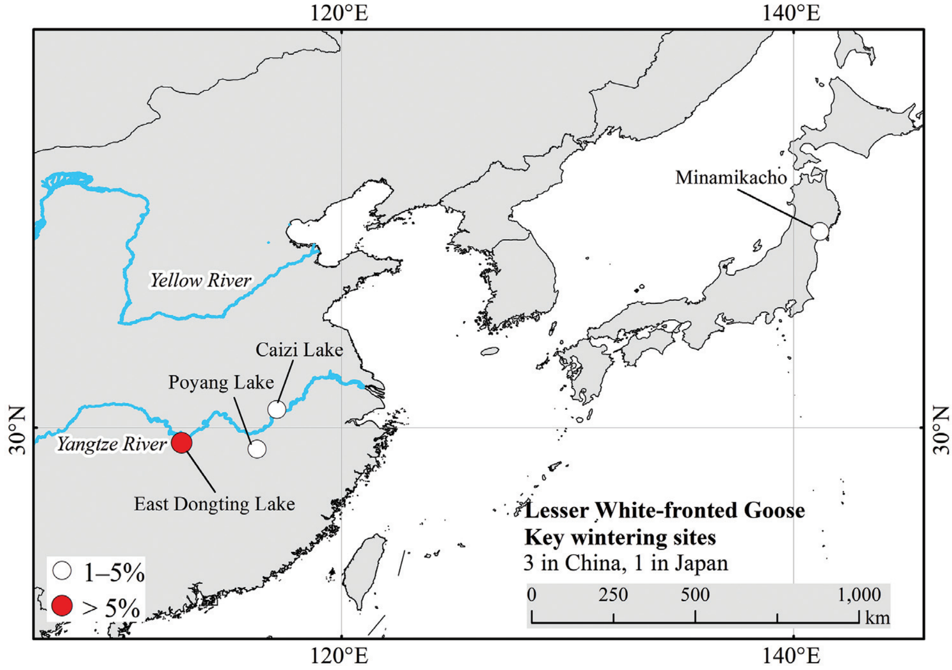

Figure 3. Map showing the four key wintering sites (1% criterion = 68 birds, white circles; 5% criterion = 340 birds, red circles) identified for the Lesser White-fronted Goose in East Asia. These include three key sites (two 1% key sites; one 5% key site) in China, and one 1% key site in Japan. The species is on the verge of extinction as a wintering species in South Korea, so no key site was located for this wintering group. The 1% and 5% thresholds were based on the maximum numbers recorded (*i.e.* total of 6,800 geese estimated for Eastern Palearctic population) during the 2015/16–2019/20 winter surveys (see Table 1 for details).

wintering sites for Lesser White-fronted Geese in recent years (207 birds in 2019 January, Table 2), numbers were lower in previous years with, for instance, only nine birds counted in 2003/04 scattered around the lake. There were almost no Lesser White-fronted Geese at Shengjin and Caizi Lake in 2003/04, but numbers there have increased subsequently to 151 in Caizi Lake in 2019/20 (Table 2, Fig. 5). Numbers at Shengjin Lake peaked at 1,713 in Shengjin Lake in 2009/10, but then fell back to 0 in 2019/20 (Table 2).

Autumn and spring migrations

In total, 13 full autumn migration and six full spring migration tracks were obtained in 2018 and 2019 from nine tagged Lesser White-fronted Geese (Fig. 6, Table 4). These birds summered in the Rauchua River catchment, southern Omulyakn Bay and eastern Russia, moulted in southern Omulyakn Bay and along the Malaya Kuropatochya River near western Kolyma Gulf, wintered on the Yangtze River floodplain (East Dongting Lake, Poyang Lake and Shengjin Lake), and mainly staged

Table 2. Annual maximum counts of Lesser White-fronted Goose at key wintering sites (n = 4) in China (one with ≥ 5% of total counts in winter 2003/04; two with ≥ 1% of total counts and one with ≥ 5% of total counts in winter 2019/20) and in Japan (one with ≥ 1% of total counts during the January 2020 survey) during December–February. The geese mostly wintered in East Dongting Lake until 2015, but numbers there have declined, whilst more modest numbers have started to use Poyang and Caizi Lakes in the period from 2017/18–2019/20. Bold font indicates maximum numbers counted at each site.

ID	Province	Wetlands	2003/04	2004/05	2005/06	2007/08	2008/09	2009/10	2010/11	2011/12
C1	Hunan	East Dongting Lake	**16,923**	8,636	2,970	15,234	10,216	16,748	24,133	–
C2	Jiangxi	Poyang Lake	9	0	–	–	–	–	–	–
C3	Anhui	Shengjin Lake	0	0	–	–	12	**1,713**	154	94
C4	Anhui	Caizi Lake	0	0	–	–	–	0	0	–
J1	Miyagi	Minamikacho	0	0	–	–	–	–	–	–

ID	Province	Wetlands	2012/13	2013/14	2014/15	2015/16	2016/17	2017/18	2018/19	2019/20
C1	Hunan	East Dongting lake	–	–	–	5,372	–	3,969	2,124	3,735
C2	Jiangxi	Poyang Lake	–	–	–	0	–	121	**207**	81
C3	Anhui	Shengjin Lake	366	0	50	0	–	0	26	0
C4	Anhui	Caizi Lake	–	–	0	0	–	0	0	**151**
J1	Miyagi	Minamikacho	–	–	–	107	134	167	200	**307**

Table 3. Summary of wetlands in the Yangtze River floodplain surveyed during January–February in winters 2003/04, 2004/05, 2015/16, 2017/18, 2018/19, 2019/20, where Lesser White-fronted Geese were recorded, showing the numbers and proportions of this species counted at each. Out of a total of 41 wetlands surveyed in winter 2003/04, three were found to support Lesser White-fronted Geese, of which two supported ≥ 1% (*i.e.* qualified as key wintering sites) and one ≥ 5% of the total population estimate. During winter 2019/20, which included increased survey coverage based on the satellite tracking data, a total of 76 wetlands were surveyed, three of which were found to support Lesser White-fronted Geese, two with ≥ 1% and one with ≥ 5% of the total population estimate. The percentage of total survey wetlands with Lesser White-fronted Geese is the proportion of total number of wetlands with this species in relation to the total number of wetlands visited during the survey.

Winter	Yangtze River		Wetlands with Lesser White-fronted Geese			Total number of Lesser White-fronted Geese
	Total no. wetlands surveyed with no Lesser White-fronted Geese	Total no. wetlands surveyed with Lesser White-fronted Geese	No. wetlands surveyed with < 1% Lesser White-fronted Goose population (< 68 birds)	No. wetlands with 1–5% of the Lesser White-fronted Goose population (68–340 birds)	No. wetlands with ≥ 5% of the Lesser White-fronted Goose population (≥ 340 birds)	
2003/04	38	3 (7%)	2 (67%)	0 (0%)	1 (33%)	16,937
2004/05	74	1 (1%)	0 (0%)	0 (0%)	1 (100%)	8,636
2015/16	72	1 (1%)	0 (0%)	0 (0%)	1 (100%)	5,372
2017/18	81	2 (2%)	0 (0%)	1 (50%)	1 (50%)	4,090
2018/19	76	3 (4%)	1 (33%)	1 (33%)	1 (33%)	2,357
2019/20	72	4 (5%)	1 (25%)	2 (50%)	1 (25%)	4,020

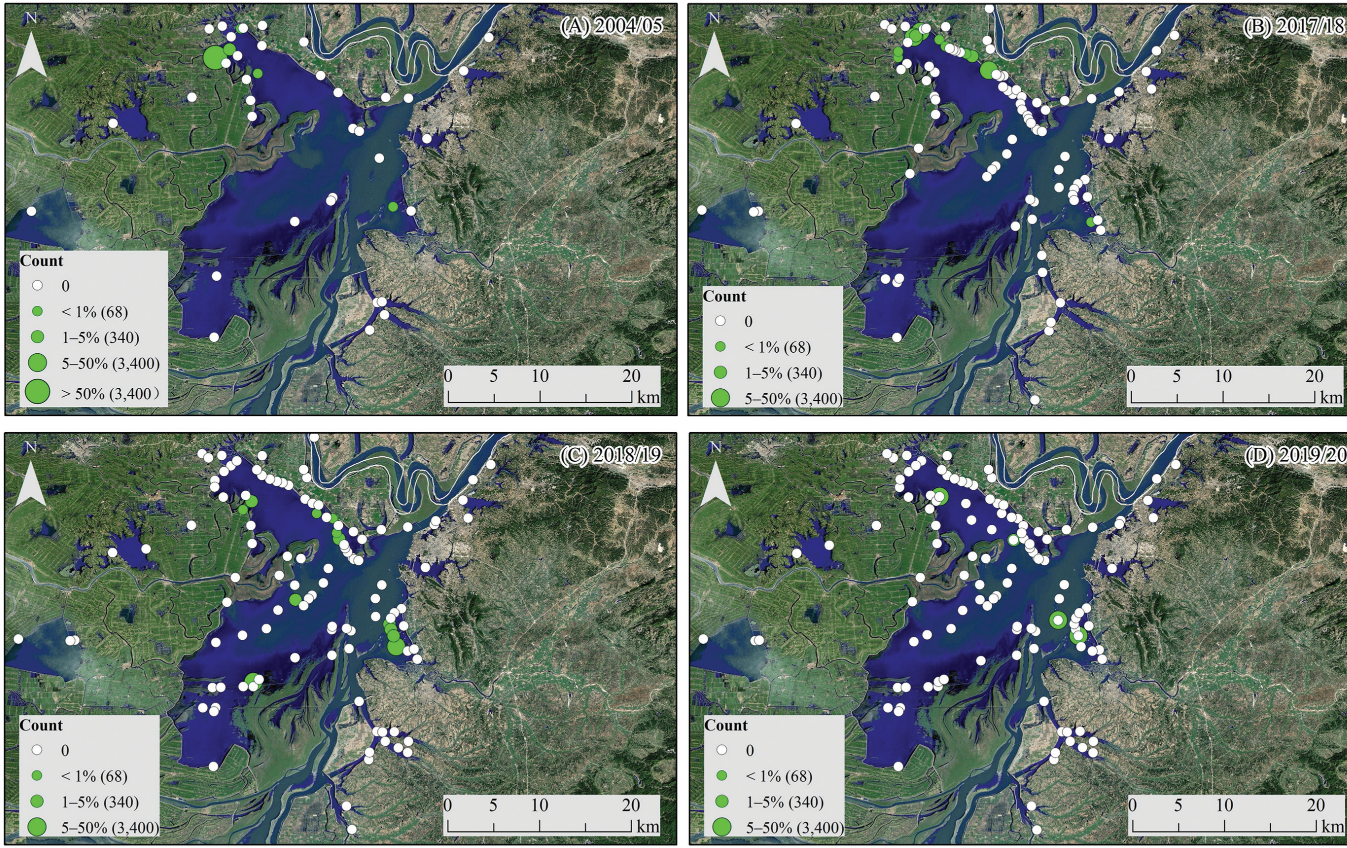

Figure 4. Fine-scale distribution of Lesser White-fronted Geese within East Dongting Lake, China, in: (A) 2004/05, (B) 2017/18, (C) 2018/19 and (D) 2019/20. White circles = sites counted but no Lesser White-fronted Geese were present (*i.e.* zero counts); size of the green circles = numbers counted, as a proportion of the total population estimate for the Eastern Palearctic population.

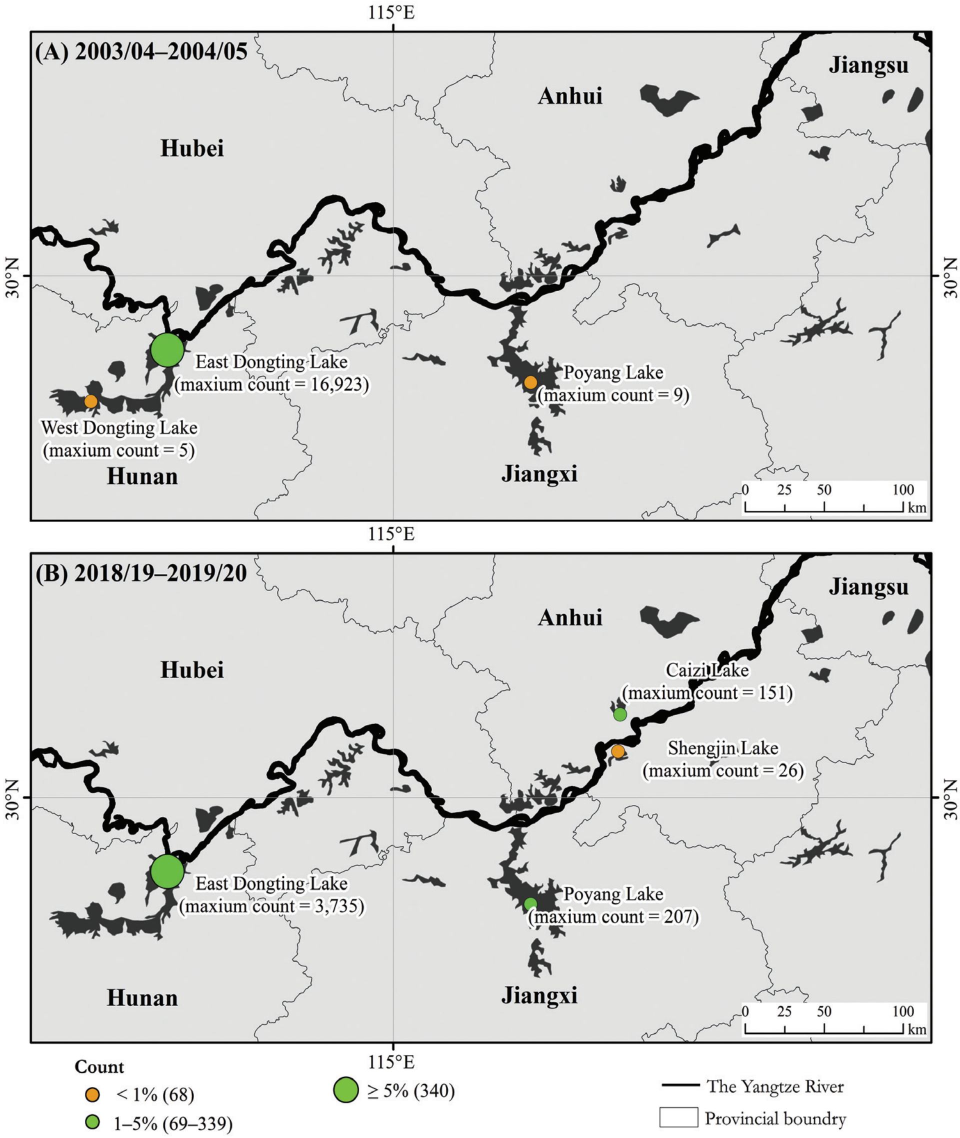

Figure 5. Changes in the numbers and distribution of Lesser White-fronted Geese at key wintering sites in the Yangtze River floodplain, China. (A) Three key wintering sites (two with ≥ 1% and one with ≥ 5% of the flyway population) in 2003/04–2004/05. (B) Two key wintering sites (one with ≥ 1% and one with ≥ 5% of the flyway population) in 2015/16 and 2017/18–2019/20. The maps show that, in recent years, the main wintering areas have spread from Hunan Province to Jiangxi and Anhui Provinces, whilst numbers wintering at East Dongting Lake have declined. Green point size is ranked according to the new population estimates (6,800 individuals, Table 1).

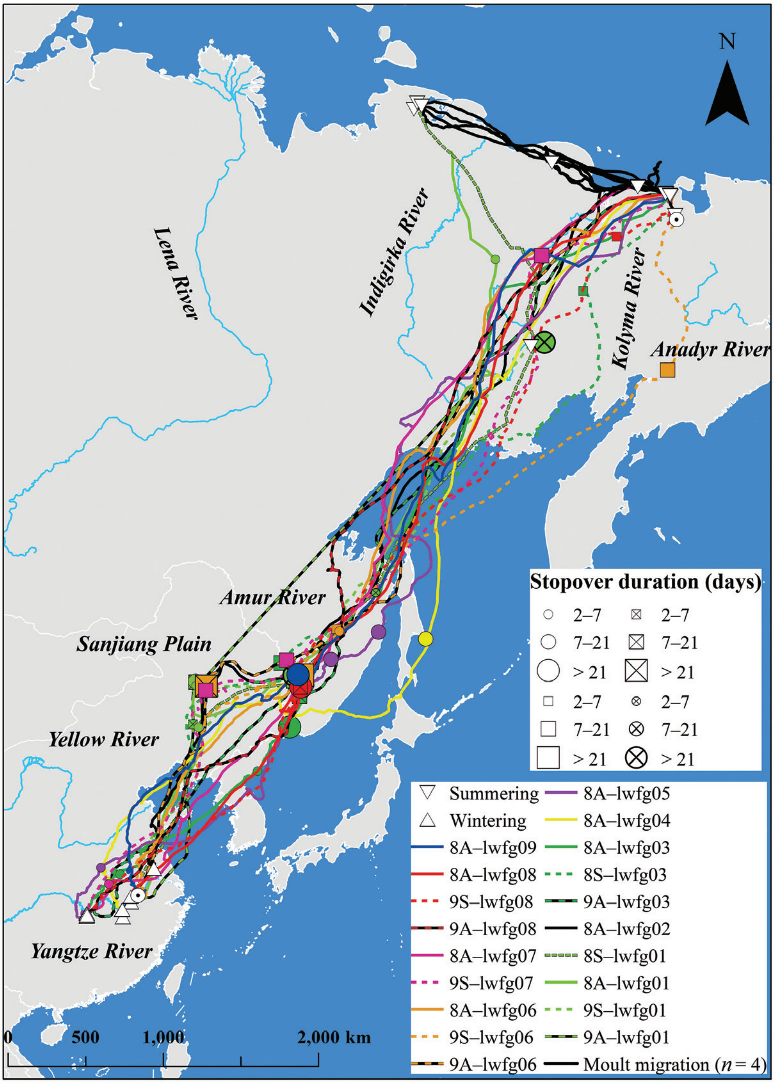

Figure 6. Autumn and spring migration routes for eight Lesser White-fronted Geese caught on the Rauchua River, arctic Russia and one in the Yangtze River floodplain in winter (suffix 01) in 2018 and 2019, including 13 complete autumn migrations and six complete spring migrations of the nine tracked geese using GPS/GSM telemetry devices. Upward pointing triangles = wintering areas (Dongting Lake, 59%; Poyang Lake, 20%; Shengjin Lake, 21%), and downward pointing triangles = summering areas for individuals. Black solid lines = return moult migrations during summer 2019 (*n* = 4; birds: 03, 06, 07 and 08). Circles and squares = stopover sites in autumn and spring, respectively; their size corresponds to stopover duration. Prefix "A" in 8A–lwfg01 and 9A–lwfg01 = the autumn migrations of individual lwfg01 in 2018 and 2019; "S" = spring migration; "8" or "9" = 2018 or 2019.

Table 4. Migration parameters of the autumn and spring migrations for individual Lesser White-fronted Geese, based on 13 complete autumn migrations and six complete spring migrations (n = 9 tracked geese).

Bird ID	Year	Season	Departure (UTC)	Arrival (UTC)	Migration duration (days)	Migration distance (km)	Migration speed (km/day)	Travel days (d)	Travel speed (km/day)	Step length (km)	No. of migration legs	No. of stopover sites	Stopover duration (days)
Spring													
lwfg01	2018	Spring	25/03/18	30/06/18	97.0	6,259.5	64.5	11.1	562.7	1,251.9	5	4	85.9
lwfg01	2019	Spring	23/03/19	25/05/19	62.4	5,309.1	85.1	14	378.1	2,654.6	2	1	48.4
lwfg02	2019	Spring	25/03/19	22/05/19	57.7	6,918.5	119.9	8.1	856.9	1,383.7	5	4	49.6
lwfg06	2019	Spring	23/03/19	26/05/19	63.8	6,361.8	99.7	4.3	1,463.5	1,590.5	4	3	59.5
lwfg07	2019	Spring	25/03/19	24/05/19	60.4	7,009.4	116	6.2	1,129.1	1,168.2	6	5	54.2
lwfg08	2019	Spring	04/04/19	28/05/19	54.1	6,439.2	119	14.5	443	2,146.4	3	2	39.6
Mean			–	–	65.9	6,382.9	100.7	9.7	805.5	1,699.2	4.2	3.2	56.2
s.e.			–	–	6.4	248.4	9.1	1.7	174.5	238.5	0.6	0.6	6.5
Autumn													
lwfg01	2018	Autumn	20/09/18	02/11/18	42.8	6,775.0	158.2	8.9	759.5	1,129.2	6	5	33.9
lwfg01	2019	Autumn	30/09/19	27/10/19	27.0	4,794.5	177.6	7.9	605.6	1,598.2	3	2	19.1
lwfg02	2018	Autumn	07/10/18	06/11/18	29.8	5,995.5	201.5	10.5	572.0	1,199.1	5	4	19.3
lwfg03	2018	Autumn	08/10/18	19/11/18	42.6	6,694.3	157.1	7.1	938.5	1,338.9	5	4	35.5
lwfg03	2019	Autumn	27/09/19	04/11/19	38.7	6,837.6	176.8	5.2	1,314.4	2,279.2	3	2	33.5
lwfg04	2018	Autumn	09/10/18	20/11/18	42.0	7,601.0	180.8	12.2	624.0	2,533.7	3	2	29.9
lwfg05	2018	Autumn	09/10/18	22/11/18	44.1	7,759.6	176.0	9.8	790.1	1,551.9	5	4	34.3
lwfg06	2018	Autumn	09/10/18	07/11/18	29.0	6,226.4	214.5	6.7	925.0	2,075.5	3	2	22.3
lwfg06	2019	Autumn	22/09/19	01/11/19	40.1	6,327.8	157.9	11.1	570.5	3,163.9	2	1	29.0
lwfg07	2018	Autumn	05/10/18	23/11/18	49.1	6,349.1	129.2	7.2	885.1	2,116.4	3	2	42.0
lwfg08	2018	Autumn	09/10/18	13/11/18	35.2	5,780.7	164.1	4.3	1,351.6	2,890.3	2	1	31.0
lwfg08	2019	Autumn	27/09/19	19/10/19	22.6	6,452.6	285.8	5.3	1,212.2	3,226.3	2	1	17.3
lwfg09	2018	Autumn	09/10/18	07/11/18	29.1	6,905.1	237.5	7.0	985.2	3,452.6	2	1	22.1
Mean			–	–	36.2	6,499.9	185.9	7.9	887.2	2,196.5	3.4	2.4	28.4
s.e.			–	–	2.2	211.8	11.3	0.7	75.6	224.2	0.4	0.4	2.1

on migration in the lower reaches of Kolyma River, Amur River in Russia and northeast China (Fig. 6).

The mean autumn departure date from the summering areas was 3 October (range = 22 September–9 October) and the mean arrival date to the winter quarters was 8 November (range = 19 October–23 November), with a mean migration duration of 36.3 days (range = 22.6–49.1 days). The tagged geese used an average of 2.4 stopover sites (range = 1–5) for between 17.3–42.0 days during autumn migration. Mean migration distance was 6,499.9 km (range = 4,794.5–7,759.6 km), while mean migration speed was 185.9 km/day (range = 157.1–285.8 km/day). The mean number of travel days was 7.9 days (range = 4.3–12.2 days) in a mean of 3.4 legs (range = 2–6 legs) of mean length 2,196.5 km (range = 1,129.2–3,452.6 km). Mean travel speed was 887.2 km/day (range = 570.5–1,351.6 km/day; Table 4).

Mean spring departure date was 26 March (range = 23 March–4 April), mean arrival date in the summering range was 31 May (range = 22 May–30 June) and mean migration duration was 65.9 days (range = 54.1–97.0 days). The tagged geese used an average of 3.2 stopover sites (range = 1–5) for between 39.6 and 85.9 days during spring migration. Mean migration distance was 6,382.9 km (range = 5,309.1–7,009.4 km), while mean migration speed was 100.7 km/day (64.5–119.9 km/day). The mean number of travel days was 9.7 (range = 4.3–14.5) in a mean of 4.2 legs (range = 2–6 legs) of mean length 1,699.2 km (range = 1,168.2–2,654.6 km). Mean travel speed was 805.5 km/day (range = 378.1–1,463.5 km/day; Table 4).

The best fit linear mixed model revealed significant effects of season and year, *i.e.* significant differences between spring and autumn migration, for three parameters (Table 5). Migration duration ($\beta = 34.57$, $t = 7.18$, $P < 0.05$) and stopover duration ($\beta = 32.13$, $t = 6.80$, $P < 0.05$) were significantly greater in spring than autumn. Migration speed ($\beta = -90.00$, $t = -5.58$, $P < 0.05$) in spring was significantly slower than that in autumn.

Land use and conservation status at stopover sites

In autumn 2018 and 2019, Lesser White-fronted Geese (9 individuals, 31 stopover sites, mean ± s.d. = 3,334 ± 2,363 fixes/individual) mainly used cultivated land (44.6%), grassland (22.4%) and water bodies (26.4%, Fig. 7). During the autumn period of 2017 and 2018, 27.4% of the tracking fixes during staging were within protected areas (Table 6), including the Qixing River National Nature Reserve (NNR), Momoge NNR, Naoli River NNR, Sanhuanpao NNR, Shengjin Lake NNR, Tumuji NNR and the Xingkai Lake NNR in China, and also the Hutinsky Zakaznik and the Poronaisky Nature Reserve in Russia (Table 6, Fig. 8).

In winter 2018/19, Lesser White-fronted Geese (9 individuals, mean ± s.d. = 9,863 ± 5,001 fixes/individual) used water bodies (65.5%) and cultivated land (29.2%, Fig. 7); 87.1% of the tracking fixes were within protected areas in China, including East Dongting Lake NNR, Poyang Lake NNR, Poyang Lake Nanji Wetland NNR and the Shengjin Lake NNR (Table 6, Fig. 8).

Table 5. Full linear mixed model effects table to predict nine migration parameters in autumn and spring of 2018 and 2019, based on 13 complete autumn migrations and six complete spring migrations of nine tracked Lesser White-fronted Geese. Migration duration and stopover duration were significantly greater in spring than the autumn. Migration speed in spring was significantly slower than that in autumn.

Parameter	Estimate	s.e.	t value	*P* value
Migration duration (days)				
Intercept	34.32	6.34	5.41	< 0.001
Factor (season) spring	34.57	4.81	7.18	0.002
Migration distance (km)				
Intercept	6,531.73	192.15	33.99	< 0.001
Factor (season) spring	4.66	156.35	0.03	0.9777
Migration speed (km/day)				
Intercept	187.71	12.04	15.59	< 0.001
Factor (season) spring	–90.00	16.14	–5.58	0.0051
Travel days (days)				
Intercept	7.85	0.87	8.97	< 0.001
Factor (season) spring	1.82	1.56	1.17	0.307
Travel speed (km/day)				
Intercept	887.31	90.33	9.82	< 0.001
Factor (season) spring	–81.81	160.74	–0.51	0.6376
Step length (km)				
Intercept	2,246.32	279.78	8.03	< 0.001
Factor (season) spring	–633.57	386.54	–1.64	0.1765
Number of migration legs				
Intercept	3.41	0.44	7.82	< 0.001
Factor (season) spring	0.82	0.59	1.39	0.2362
Number of stopover sites				
Intercept	2.41	0.44	5.52	< 0.001
Factor (season) spring	0.82	0.59	1.39	0.2362
Stopover duration (days)				
Intercept	26.50	5.75	4.61	< 0.001
Factor (season) spring	32.13	4.72	6.80	0.0024

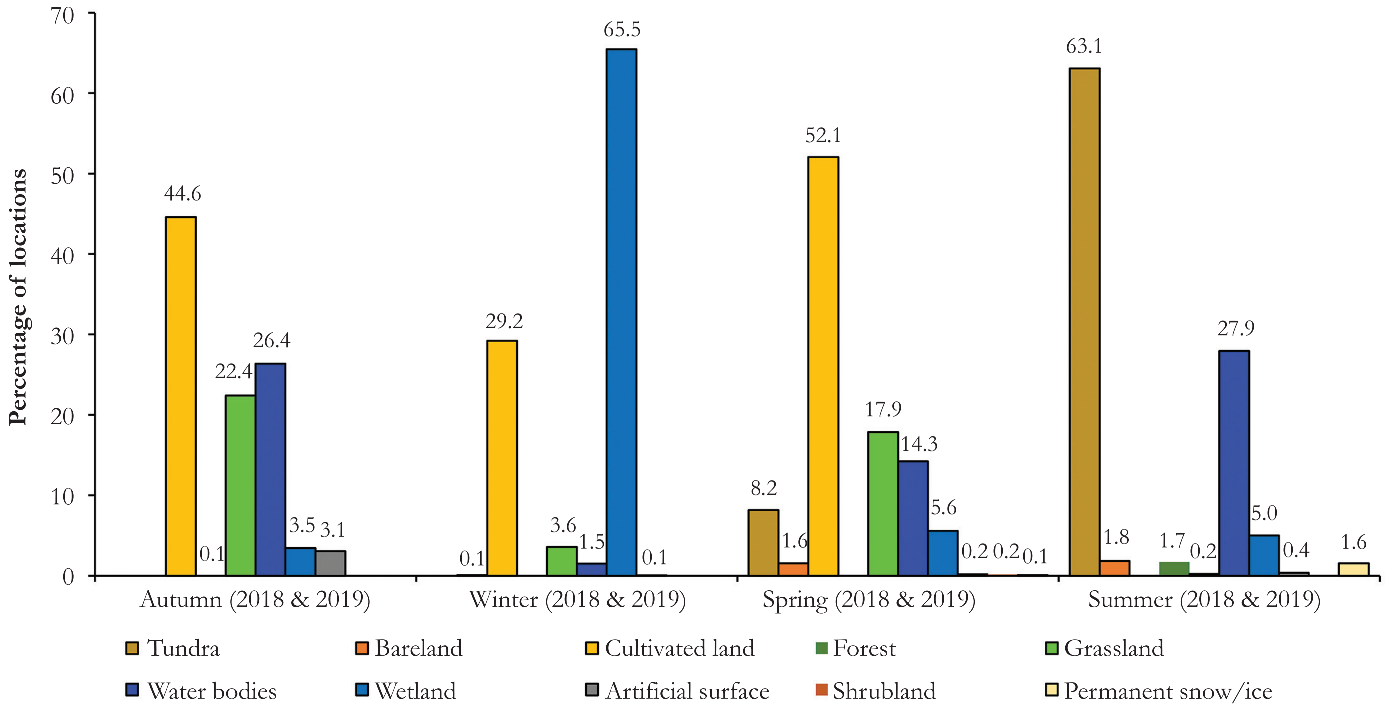

Figure 7. Land use type used by Lesser White-fronted Geese at stopover sites in spring (five individuals, 19 stopover sites, 6,457 ± 2,081 fixes/individual), autumn (nine individuals, 31 stopover sites, 3,334 ± 2,363 fixes/individual), summer (nine individuals, 16,678 ± 10,400 fixes/individual) and winter (nine individuals, 9,863 ± 5,001 fixes/individual), based on individual tracking data at stopover sites in 2018 and 2019.

Table 6. Percentage of locations within protected areas, and timing of stopovers, for nine Lesser White-fronted Geese which summered in Russia and wintered in China between 2018 and 2019, based on GPS fixes during autumn stopover periods in 2018 and 2019, winters in 2018/19 and 2019/20, spring stopover periods in 2018 and 2019 and summers 2018 and 2019.

Bird ID	Year	Season	Arrival	Departure	Duration (days)	Total no. of fixes	No. of fixes within protected areas	Percentage in protected areas	Protected areas occupied
lwfg01	2018	Autumn	21/09/2018	27/09/2018	6.0	134	0	0%	
lwfg01	2018	Autumn	03/10/2018	18/10/2018	15.8	324	312	96%	Tumuji
lwfg01	2018	Autumn	18/10/2018	23/10/2018	4.3	86	0	0%	
lwfg01	2018	Autumn	23/10/2018	27/10/2018	3.9	86	0	0%	
lwfg01	2018	Autumn	28/10/2018	01/11/2018	4.0	88	88	100%	Shengjin Lake
lwfg01	2019	Autumn	05/10/2019	22/10/2019	17.0	337	317	94%	Tumuji
lwfg01	2019	Autumn	22/10/2019	24/10/2019	2.1	43	0	0%	
lwfg02	2018	Autumn	11/10/2018	16/10/2018	4.8	60	0	0%	
lwfg02	2018	Autumn	17/10/2018	21/10/2018	3.8	82	82	100%	Naoli River
lwfg02	2018	Autumn	24/10/2018	26/10/2018	2.9	61	0	0%	
lwfg02	2018	Autumn	27/10/2018	04/11/2018	7.8	594	594	100%	Momoge
lwfg03	2018	Autumn	12/10/2018	14/10/2018	2.3	45	0	0%	
lwfg03	2018	Autumn	14/10/2018	06/11/2018	22.9	2,981	0	0%	
lwfg03	2018	Autumn	07/11/2018	11/11/2018	4.0	469	0	0%	
lwfg03	2018	Autumn	13/11/2018	19/11/2018	6.3	711	0	0%	
lwfg03	2019	Autumn	29/09/2019	17/10/2019	18.0	1,867	1,256	67%	Xingkai Lake
lwfg03	2019	Autumn	18/10/2019	02/11/2019	15.5	1,801	37	2%	Naoli River, Qixing River

lwfg04	2018	Autumn	12/10/2018	31/10/2018	18.2	2,471	2,471	100%	Poronaisky
lwfg04	2018	Autumn	02/11/2018	14/11/2018	11.6	984	141	14%	Sanhuanpao, Qixing River
lwfg05	2018	Autumn	12/10/2018	21/10/2018	9.1	1,216	104	9%	Hutinsky
lwfg05	2018	Autumn	21/10/2018	29/10/2018	7.7	559	0	0%	
lwfg05	2018	Autumn	31/10/2018	11/11/2018	11.0	1,105	0	0%	
lwfg05	2018	Autumn	14/11/2018	20/11/2018	6.4	726	0	0%	
lwfg06	2018	Autumn	12/10/2018	14/10/2018	2.5	74	0	0%	
lwfg06	2018	Autumn	15/10/2018	04/11/2018	19.8	1,301	550	42%	Naoli River, Qixing River
lwfg06	2019	Autumn	30/09/2019	29/10/2019	29.0	3,198	376	12%	Momoge
lwfg07	2018	Autumn	10/10/2018	14/11/2018	35.0	1,770	627	35%	Naoli River
lwfg07	2018	Autumn	16/11/2018	23/11/2018	6.9	625	6	1%	
lwfg08	2018	Autumn	12/10/2018	12/11/2018	31.0	1,189	0	0%	Xingkai Lake
lwfg08	2019	Autumn	30/09/2019	17/10/2019	17.3	2,288	0	0%	
lwfg09	2018	Autumn	12/10/2018	04/11/2018	22.1	933	779	83%	Naoli River, Qixing River
lwfg01	2018	Spring	30/03/2018	12/05/2018	43.3	887	383	43%	Naoli River, Sanhuanpao, Qixing River
lwfg01	2018	Spring	13/05/2018	15/05/2018	1.8	39	0	0%	
lwfg01	2018	Spring	15/05/2018	17/05/2018	2.2	46	0	0%	
lwfg01	2018	Spring	21/05/2018	29/06/2018	38.6	913	224	25%	Sugoj Zakaznik
lwfg01	2019	Spring	25/03/2019	12/05/2019	48.4	1,025	609	59%	Naoli River, Sanhuanpao, Qixing River
lwfg03	2019	Spring	27/03/2019	02/04/2019	6.8	891	885	99%	Momoge
lwfg03	2019	Spring	03/04/2019	25/04/2019	22.7	2,963	2,261	76%	Naoli River, Sanhuanpao, Qixing River
lwfg03	2019	Spring	25/04/2019	10/05/2019	14.5	1,949	0	0%	
lwfg03	2019	Spring	16/05/2019	21/05/2019	5.6	752	752	100%	Omolonskiy

Table 6 (*continued*).

Bird ID	Year	Season	Arrival	Departure	Duration (days)	Total no. of fixes	No. of fixes within protected areas	Percentage in protected areas	Protected areas occupied
lwfg06	2019	Spring	25/03/2019	07/05/2019	43.2	5,550	3,760	68%	Naoli River, Qixing River, Sanhuanpao, Raohe Northeast Black Bee
lwfg06	2019	Spring	08/05/2019	10/05/2019	2.7	329	0	0%	Bolon'sky
lwfg06	2019	Spring	12/05/2019	25/05/2019	13.6	1,864	0	0%	
lwfg07	2019	Spring	27/03/2019	09/04/2019	13.8	1,771	1,619	91%	Momoge
lwfg07	2019	Spring	10/04/2019	15/04/2019	5.6	695	126	18%	Naoli River, Qixing River
lwfg07	2019	Spring	15/04/2019	27/04/2019	11.6	1,535	54	4%	Naoli River, Qixing River
lwfg07	2019	Spring	27/04/2019	12/05/2019	14.7	1,900	1,131	60%	Naoli River, Qixing River
lwfg07	2019	Spring	15/05/2019	23/05/2019	8.6	1,185	0	0%	
lwfg08	2019	Spring	07/04/2019	11/05/2019	34.5	4,611	3,348	73%	Sanhuanpao, Qixing River
lwfg08	2019	Spring	22/05/2019	28/05/2019	5.1	681	0	0%	
lwfg01	2019	Summer	25/05/2019	30/09/2019	128.0	2,764	2,175	79%	Sededema Zakaznik, Sylgy-Yta Zakaznik, Sugoj Zakaznik
lwfg02	2018	Summer	24/07/2018	07/10/2018	75.3	8,395	0	0%	
lwfg03	2018	Summer	17/07/2018	08/10/2018	83.2	10,930	0	0%	
lwfg03	2019	Summer	22/05/2019	27/09/2019	127.9	17,890	38	0%	Ozero Bol"shoe Morskoe, Kytalyk, Kolyma-Koren, Chajgurgino

lwfg04	2018	Summer	21/07/2018	09/10/2018	80.3	9,778	0	0%	
lwfg05	2018	Summer	03/08/2018	09/10/2018	67.3	8,410	0	0%	
lwfg06	2018	Summer	22/07/2018	09/10/2018	79.2	10,184	0	0%	
lwfg06	2019	Summer	26/05/2019	22/09/2019	118.3	16,393	3,624	22%	Chajgurgino
lwfg07	2018	Summer	31/07/2018	05/10/2018	66.8	8,128	0	0%	
lwfg07	2019	Summer	24/05/2019	26/09/2019	124.4	17,354	3,014	17%	Kytalyk, Kolyma-Koren, Chajgurgino
lwfg08	2018	Summer	27/07/2018	09/10/2018	74.3	9,408	0	0%	
lwfg08	2019	Summer	28/05/2019	27/09/2019	121.6	16,928	698	4%	Kolyma–Koren, Chajgurgino
lwfg09	2018	Summer	19/07/2018	09/10/2018	82.3	10,745	0	0%	
lwfg01	2018	Winter	02/11/2018	23/03/2019	141.5	451	347	77%	East Dongting Lake, Shengjin Lake, Poyang Nanji Wetland
lwfg02	2018	Winter	06/11/2018	08/11/2018	2.6	298	0	0%	
lwfg03	2018	Winter	19/11/2018	25/03/2019	125.7	27,358	27,138	99%	East Dongting Lake
lwfg04	2018	Winter	20/11/2018	24/03/2019	124.7	23,856	18,432	77%	East Dongting Lake, Poyang Lake
lwfg05	2018	Winter	22/11/2018	25/03/2019	123.1	21,300	20,902	98%	East Dongting Lake
lwfg06	2018	Winter	07/11/2018	23/03/2019	136.7	30,102	29,014	96%	East Dongting Lake, Shengjin Lake, Poyang Nanji Wetland, Poyang Lake
lwfg07	2018	Winter	23/11/2018	25/03/2019	121.5	18,118	18,118	100%	East Dongting Lake
lwfg08	2018	Winter	13/11/2018	04/04/2019	141.9	29,802	26,710	90%	East Dongting Lake, Shengjin Lake
lwfg09	2018	Winter	07/11/2018	01/01/2019	55.1	10,902	544	5%	East Dongting Lake, Poyang Nanji Wetland

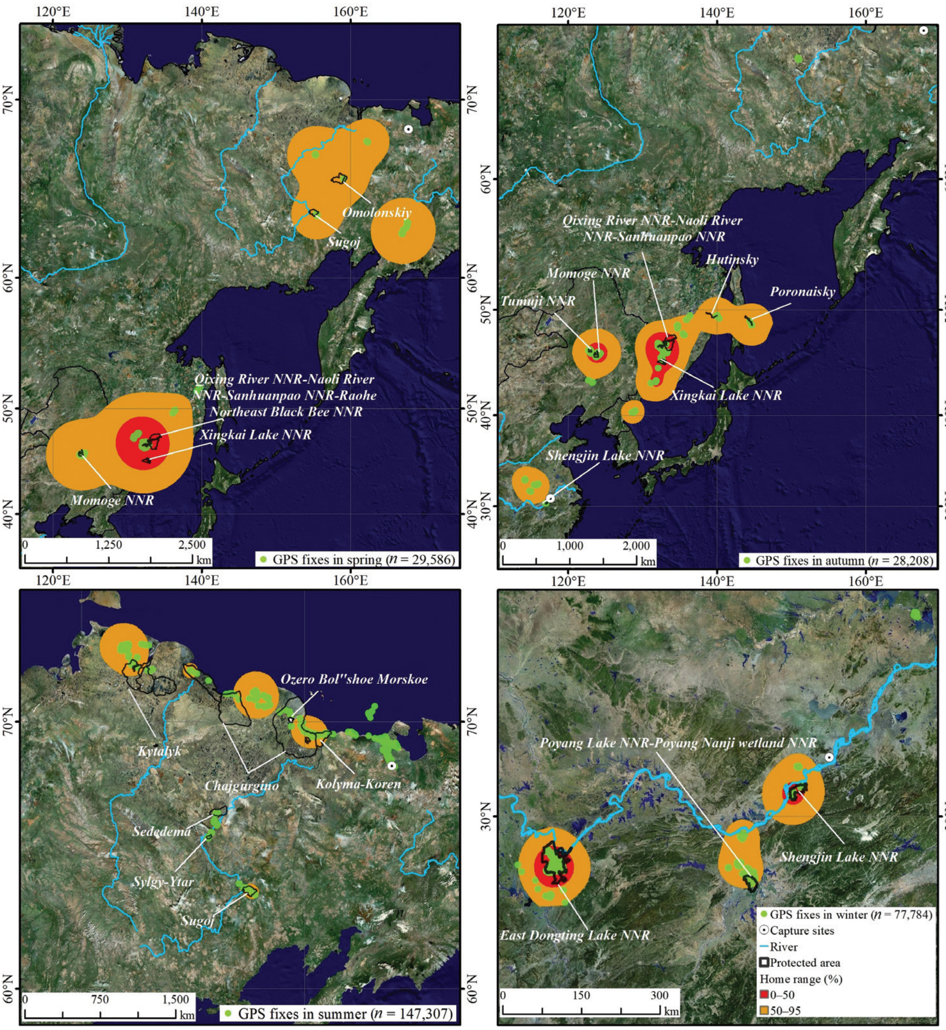

Figure 8. Use of protected areas by nine tagged Lesser White-fronted Geese, which bred in Russia and wintered in China between 2018 and 2019. The analysis is based on GPS fixes during autumn 2018 and 2019 (nine individuals, 31 stopover sites, mean ± s.d. = 910 ± 911 fixes/site), winter 2018 and 2019 (nine individuals, 8,643 ± 5,607 s.d. fixes/winter), summer 2018 and 2019 (nine individuals, 11,331 ± 4,518 s.d. fixes/summer) and in spring 2018 and 2019 (five individuals, 19 stopover sites, 1,557 ± 1,446 s.d. fixes/site). Black borders indicate the protected areas Lesser White-fronted Geese occupied, identified by name in white text. The home range areas (shown as 0–50% Kernal Density Estimation in red, 50–95% in orange, see *Methods* for details) we recommend should be investigated for designation of future protected areas for the species. During summer, autumn stopovers, winter and spring stopovers, 6.5%, 27.4%, 87.1% and 51.2%, respectively of the GPS fixes were in protected areas.

In spring 2018 and 2019, Lesser White-fronted Geese (5 individuals, 19 stopover sites, 6,457 ± 2,081 fixes/individual) mainly used cultivated land (52.1%), grassland (17.9%) and water bodies (14.3%, Fig. 7). During springs 2017 and 2018, 51.2% of the tracking fixes were within protected areas, including the Baoqing River National Nature Reserve, Momoge National Nature Reserve, Naoli River National Nature Reserve, Raohe Northeast Black Bee National Nature Reserve and the Sanhuanpao National Nature Reserve in China, and the Omolonskiy Zakaznik and Sugoj Zakaznik in Russia (Table 6, Fig. 8).

In summer 2018 and 2019, Lesser White-fronted Geese (9 individuals, 16,678 ± 10,400 fixes/individual) mainly used tundra (63.1%), water bodies (27.9%) and wetland (5.0%, Fig. 7). During this period, 6.5% of the tracking fixes were within protected areas in Russia, including the Chajgurgino Resource Reserve, Kolyma-Koren Resource Reserve, Kytalyk National Park, Ozero Bol''shoe Morskoe Protected Area, the Sededema Zakaznik, Sugoj Zakaznik and Sylgy-Ytar Zakaznik (Table 6, Fig. 8).

Discussion

Distribution and migration range

New data has enabled the redefinition of the wintering distribution of Lesser White-fronted Geese, based on wintering counts, satellite tracking data and expert knowledge in all range states. The wintering distribution remained largely unchanged, but was somewhat reduced in extent, and is considered now to be confined largely to the middle and lower reaches of the Yangtze River, excluding the formerly occupied coastal areas of Guangxi and Fujian Provinces (Fig. 1). We were unable to make major changes to our knowledge of the extent of the summering area because of data limitations and deficiencies in available information. We continue to urge for more telemetry studies of this iconic and rapidly declining species to better identify the relationships between breeding, staging, moulting and wintering sites, but especially to define the breeding range, in combination with follow-up aerial survey to identify key sites and habitats occupied during the summer period.

Satellite tracking and expert knowledge confirmed the discrete nature of the East-Asian Continental & West Pacific Flyway, showing geese passing through the Amur River from Rauchua River, the Sanjiang Plain in northeast China to the Yangtze River, with spring and autumn routes roughly the same. From the study of Lei *et al.* (2019a), we extracted the distribution and spring migration routes of winter tagged Lesser White-fronted Geese, but we were unable to determine their summering areas. The fan-shaped migration track of the geese from Dongting Lake differs from the narrow corridor taken by the Rauchua River birds and confirms that these birds (caught at one location on the wintering grounds) likely dispersed to breed at low densities across a very wide geographical area within the Russian taiga and arctic biome, suggesting that the true extent of their summering areas may be considerably more extensive. Indeed, because of the highly limited number of tagged birds and restricted catching sites, the migration routes of Lesser White-fronted Geese between their breeding and wintering areas remain largely unknown. Again, in order to understand fully the flyway structure and migration routes taken by Lesser White-fronted Geese in East Asia, we urgently need more cooperative research and especially telemetry studies of birds caught both on the breeding grounds and at wintering sites.

Abundance estimates and trends in East Asia

We here sought to update the estimate of population size and trends in Lesser White-fronted Geese wintering in three countries in East Asia over the last nine years (for winters 2011/12–2019/20). Estimates of total wintering numbers based on incomplete surveys in the 1990s and comprehensive surveys in the early 2000s suggested a major decline of Lesser White-fronted Geese, and the numbers wintering in China apparently continued to decline during 2003/04 to 2019/20, almost certainly due to the loss and degradation of habitat in the Yangtze River floodplain, as described for Caisang Lake and East Dongting Lake below (Wang *et al.* 2013; Jia *et al.* 2019).

There is no doubt that the Lesser White-fronted Goose is a highly specialist feeder and its short bill and relative small body size means that the species needs to sustain very high intake rates of good quality forage to maintain a positive energy budget, typically by grazing single species swards of spikerush *Eleocharis* sp. and foxtail *Alopecurus* sp. (Wang *et al.* 2013). The niche of the Lesser White-fronted Goose therefore is more restricted than, for instance, the sympatric-wintering Bean Goose *Anser fabalis* and consequently suffers more from between-year fluctuations in food quality and availability (Lei *et al.* 2019b). These single species swards are dependent on highly specific patterns of water table recession that enable rapid sward growth on bare substrates especially in autumn and spring (Wang *et al.* 2013). It generally has been considered that these combinations of conditions are extremely rare and restricted in the Yangtze River floodplain, a feature that explained the previously highly clumped and fragmented distribution of the species in previous times (Wang *et al.* 2012). One major reason for the collapse of wintering Lesser White-fronted Geese at East Dongting Lake has undoubtedly been the loss of shallow water and mud habitat in Caisang Lake (for location see Supplementary Materials Figure S1A) since 2013 (Wang *et al.* 2013), where permanent water has been retained to support the growth of Lotus *Nelumbo nucifera* and Chinese Mitten Crab *Eriocheir sinensis* aquaculture (Zou *et al.* 2017). During 2008–2010, this one area alone supported up to 4,300 Lesser White-fronted Geese in autumn 2008 and spring 2009 (Cong *et al.* 2012), *i.e.* nearly equivalent to the total counted in the flyway population today. Numbers declined to 2,133 in 2017/18 and, following the permanent flooding, none were present there during complete coverage in 2018/19 and 2019/20. Former resorts elsewhere at East Dongting Lake were also completely deserted during the extensive count coverage in 2019 and 2020 (see Fig. 4 and Supporting Materials Fig. S1). Contemporary studies showed that Lesser

White-fronted Geese could not maintain their energy budgets when foraging far more abundant and extensive sedge *Carex* sp. swards at the same site, and lost body mass when denied access to *Eleocharis* sp. and *Alopecurus* sp. swards (Wang *et al.* 2013). Such critical loss of highly selected habitats has likely occurred elsewhere in the Yangtze River floodplain without witness, but the loss at Caisang is especially concerning to conservationists because this area is within the East Dongting Lake National Nature Reserve. It is clear that we urgently need better studies of the annual winter habitat use and diet of this species where it occurs in China, to understand the relative profitability of different dietary items and provide site managers with an understanding of how to provide the best feeding opportunities for the species through local water level and wetland management. Such knowledge is essential to balance the energy budget of the species during the winter, such that they can depart on spring migration in optimal condition (Wang *et al.* 2013).

In contrast to drastic declines on the winter quarters, increasing numbers of summering Lesser White-fronted Geese have been reported from the Rauchua River in Chukotka, from where all but one of our tracked birds originated. It is known there were no Lesser White-fronted Geese breeding in this area in 1983 (Krechmar *et al.* 1991), yet numbers reached 250 birds in 2010 (Solovyeva & Vartanyan 2011) and 491 were counted (out of an estimated 600 individuals) in 2018 (D. Solovyeva & S. Vartanyan, unpubl. data). It is difficult to believe that the relatively limited Rauchua River catchment (*c.* 320 km in length and draining a catchment of 15,400 km^2) alone supports 9% of the current estimated East Asian population, yet this seems to be the case. Other known breeding sites in Russia are associated with larger rivers with vast areas of suitable habitat and the trajectories of the tagged birds in Lei *et al.* (2019a) suggested very widespread breeding provenance, so one might expect these breeding sites to be used by more birds than those using the Rauchua River (Degtyarev & Perfiliev 1996; Artiukhov & Syroechkovskiy 1999). It also seems highly likely that there remain very many undiscovered breeding sites, which are likely in excess of the current restricted number of known sites. There is, however, no doubt that the numbers wintering in East Asia have declined dramatically in recent years.

Sixty-one per cent of GPS fixes of tracked individuals were from sites covered during the winter survey in China in January 2020 (Supporting Materials Table S4), suggesting that the total Eastern Palearctic population size could potentially be as high as 6,800 individuals. That is still however substantially lower than the estimated 16,000 based on counts from 2015 (Fox & Leafloor 2018), which also assumed 100% coverage at that time, but likely also missed geese at uncounted sites. Based on our own extensive count coverage and supplementary bird-watching data, no other large wintering sites were found in China or elsewhere in East Asia. The increase in numbers of summering birds on the Rauchua River may therefore be the result of climate change contributing to birds switching their normal summering areas, although we should be prudent not to conclude too much from this local change in abundance over the last 40 years. All of this information, coupled with our continued lack of data regarding breeding areas from tracked birds from throughout the winter range, confirms the urgent need for more tagging of Lesser White-fronted Geese in concert with follow-up comprehensive summering surveys to establish the distribution and abundance of this vulnerable species.

The increase in the modest wintering numbers in Japan since the 1970s is, by contrast, encouraging, but the numbers are extremely small and in no way balance the catastrophic losses that have occurred in China over the last 35 years. The causes for recent increases are difficult to identify given the highly specialist nature of its feeding ecology in other parts of its range (*e.g.* Karmiris *et al.* 2017), but it may be because supplementary rice has been provided to wintering wild geese of several species in Japan in recent years, and the Lesser White-fronted Goose has started to utilise this food resource (I. Toshio, pers. comm.). However, this species has not begun to use farmland or supplementary feeding to any great extent on the Chinese wintering grounds (Fig. 7, Yu *et al.* 2017), which is also a potential reason for the contrasting trends in abundance in the two countries. Nevertheless, the possibility exists that the provision of artificial food at multiple wintering sites could potentially help the species balance energy budgets at key points during the winter and should be examined at the earliest opportunity.

Key wintering sites of Lesser White-fronted Geese in China and Japan

In the 1980s, Lesser White-fronted Geese were distributed in Hunan, Hubei, Jiangxi, Anhui and Jiangsu Provinces (Wang *et al.* 2012). From winters 2003/04–2004/05, Lesser White-fronted Geese were largely restricted to Dongting Lake. Since 2016, numbers wintering at Dongting Lake have decreased dramatically (Table 2) and modest numbers began to be reported from Poyang Lake, Shengjin Lake and Caizi Lake. This pattern of initial distribution contraction, followed by outward diffusion may reflect the major loss of the food supply at East Dongting Lake (described above), forcing a small number of geese to move to areas formerly occupied within its historical distribution. Tracked geese mainly wintered in Dongting Lake (59%), Poyang Lake (20%) and Shengjin Lake (21%), while two individuals (lwfg04 and lwfg08) shifted from Poyang Lake and Shengjin Lake to Dongting Lake, and one individual (lwfg09) died while wintering in Poyang Lake. Dongting Lake is still considered to be the largest wintering site for the Lesser White-fronted Geese. However, away from studies at Caisang (where the former Lesser White-fronted Goose habitat no longer exists; Wang *et al.* 2013; Zou *et al.* 2017), we still lack any understanding of the habitat selection and foraging energetics of this rare and threatened species at Chinese-wintering sites to enlighten us about the sympathetic management of terrestrial and aquatic habitats needed to provide adequate food resources throughout the winter season, and there is an urgent need to rectify this.

Autumn and spring migration

Spring migration duration of the Lesser White-fronted Goose was longer than in autumn (Table 5). This pattern goes against expectations, because it is generally believed that birds should try to arrive as early as possible to breeding areas to access best-quality sites (Kokko 1999). More specifically, in the case of herbivorous waterbirds, they need to get ahead of the spring flush of plant growth so that their young hatch to optimal food conditions (*e.g.* Van der Graaf *et al.* 2006). Recent climate change has been especially pronounced in Chukotka (Arctic Climate Impact Assessment 2004), where all of our tracked Lesser White-Fronted Geese summered. As a result, demonstrably milder conditions now provide prolonged optimal plant growth periods, and hence improved foraging for young birds, reflected in the improved breeding success of locally-nesting Bewick's Swans *Cygnus columbianus bewickii* (Solovyeva & Vartanyan 2014). However, the rate of progress on spring migration is heavily influenced by the rate of thaw along the length of the flyway and how rapidly the birds are able to proceed given local snow cover conditions (as in the case of Bean Geese; Li *et al.* 2019). It therefore would appear that, in common with many arctic nesting goose and swan species, seasonal differences in food availability, wind conditions (Shamoun-Baranes *et al.* 2003) and patterns of snow and ice melt along the flyway corridor (Bauer *et al.* 2006; Nuijten *et al.* 2014) all conspire to affect the timing and speed of the spring migration of individual Lesser White-fronted Geese, making this migration episode longer than that in autumn. Using available remote sensing tools combined with greater sample sizes from telemetry studies, there are opportunities for further future investigation of the relationships between these environmental factors and the speed and nature of the spring and autumn migrations in Lesser White-fronted Geese within this population and throughout Eurasia.

Land use and conservation status at stopover sites

During stopovers in spring and autumn, Lesser White-fronted Geese mostly used cultivated land, water bodies and grassland, suggesting a far greater reliance on agricultural land to acquire energy and nutrients than is the case in winter, when the population is more confined to natural wetlands in China. In winter, northeast China with its highly developed agricultural landscape serves as the first really suitable feeding area after a long, almost non-stop crossing of Far Eastern Russia where there is no agriculture and permanent hunting pressure. Autumn hunting is open from late August in Chukotka and all along the migration route in Russia. This may mean that Lesser White-fronted Geese have lost natural staging areas along their flyway and have been forced to resort to farmland, or it could indicate a behavioural and dietary flexibility to adapt to novel and potentially rich food sources through choice. It is generally supposed that wintering geese in China using protected nature reserves tend not to use adjacent agricultural land because of the threat of human persecution and lack of food in such areas (Yu *et al.* 2017; Zhao *et al.* 2018), yet it was evident from the results of this study that they feed on farmland on both spring and autumn migration (Fig. 7). There is an urgent need to study the species on these staging grounds to establish their diets, available food resources, their safety at roosts and vulnerability to human activities by day, to extend site safeguard measures and instigate additional protection and sympathetic management where necessary. High reliance on agricultural land is the normal situation for swans and geese found in Europe and North America (*e.g.* Beekman *et al.* 2019; Wood *et al.* 2019) and there is a powerful argument for allowing geese to meet their energy requirements by feeding on the surplus from agriculture (*e.g.* Fox & Abraham 2017), especially for a rare species showing such a dramatic rate of decline. Only 51% of spring and 27% of autumn telemetry positions were from protected areas and, while this may have been because they were on farmland, there is still a need to understand whether the provision of sacrificial crops or other forms of protection could enhance the energetic and nutritional gains of the geese exploiting these areas in the future. We need to be better able to understand how we can enhance breeding success and survival by improving conditions at the key stopover areas, combining on-site energetic studies with telemetry data to show how and why geese select between the feeding opportunities available to them. The level of site safeguard in areas used by the tagged geese in winter was well in excess of that in spring, autumn and summer; in winter 2018/19, 87% of fixes were in protected areas. This is partly because in China the Lesser White-fronted Goose is reticent to feed outside of wetlands on the farmland (Yu *et al.* 2017), but as noted in the case of Caisang Lake, a protected area does not guarantee protection of key Lesser White-fronted Goose habitats.

Finally, many of the tracked birds disappeared during their time within Russia where the mobile phone network coverage is incomplete, so we often have little idea of the fates of geese that have disappeared. Illegal hunting remains a serious problem in Russia and Kazakhstan (where spring hunting has recently been banned) for Lesser White-fronted Geese further west in their range (Mooij 1992; Yerokhov 2013; Newth *et al.* 2019), but we currently have no idea of its magnitude and effect on the Eastern Palearctic population.

Conservation and research recommendations

The breeding areas for Lesser White-fronted Geese were located in the less-populated areas of the arctic tundra and in all likelihood in the taiga as well, although the proportion of positions from tagged birds in protected areas in summer was low. The Lesser White-fronted Goose was more concentrated in nature reserves during the wintering period, which should imply that its conservation status in winter is satisfactory. However, at Dongting Lake, the largest and traditionally most important wintering site, hydrological changes have resulted in lost food resources, degradation of habitats (see the account above and Zhang *et al.* 2018), and have likely caused the major decrease in numbers at the site.

It is essential that the former, natural hydrological processes of the wintering habitat of these geese be restored and maintained in the immediate future to safeguard the future of the species at this site. At the same time, the extent of protected areas used by the geese in spring and autumn was relatively low, when they mainly used cultivated land. For this reason, we urge local study of the feeding ecology of the species, strengthening of the protection of night-time roosts, and increased efforts to ensure that the geese have undisturbed access to cultivated land within 30 km of the reserves frequented (the Qixing River National Nature Reserve, Momoge National Nature Reserve, Naoli River National Nature Reserve, Raohe Northeast Black Bee National Nature Reserve and the Sanhuanpao National Nature Reserve).

Establishment of a coordinated long-term continuous and standardised monitoring programme on the winter quarters (especially in China) in conjunction with detailed feeding ecology studies would help to determine reasons for changes in abundance at a suite of key sites, for advising authorities on how local and regional management influences the flyway abundance of the Lesser White-fronted Goose in East Asia. Closer collaboration between monitoring, research and management interests should combine telemetry data and within-site distributional count data to assess the causes of between-site movements in relation to food profitability and availability, thus guiding improvements in habitat management. This approach will help to devise and implement targeted conservation strategies at the site, regional and flyway level for this species. More extensive telemetry studies will continue to identify important habitats and fill gaps in knowledge of the conservation measures required for Lesser White-fronted Geese in East Asia.

Acknowledgements

We gratefully acknowledge the contribution of the fieldwork teams in China (Fang Lei and Li Xianghuang) and Russia (Gleb Danilov, Sent Pier Josephina de Vilmont, Carlie Strancki and Thomas Ogilvi) for their contributions, and also the survey teams, especially Wang Lanhua. Logistics and transportation to remote Rauchua River were provided by the Chukotka Gold Mining Company, a subsidiary of Kinross Gold. The study was supported by the National Natural Science Foundation of China (Grants Nos. 31670424, 31970433, 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), the China Biodiversity Observation Networks (Sino BON) and the Youth Innovation Promotion Association (No. 2020046), Chinese Academy of Sciences. Funders had no role in study design, data collection and analysis, decision to publish, or manuscript preparation. Approval for bird capture and transmitter deployment was obtained from Russia (Federal Service for Technical and Export Control, Ref. No. 320; Ministry of Natural Resources, Ref. No. 058) and China (Anhui Provincial Forestry Bureau, Ref. No. 2016178), as well as from the Animal Ethics Committee at the Research for Eco-environmental Sciences, Chinese Academy of Sciences. Two anonymous referees made helpful comments on a draft of the text.

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