

Contrasting trends in two East Asian populations of the Greater White-fronted Goose *Anser albifrons*

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Abstract

East Asian Greater White-fronted Goose *Anser albifrons* populations are less well defined and monitored than those in Europe and North America. Here, we combine historical and newly-reported telemetry data, wintering waterbirds surveys and expert advice to synthesis and update our knowledge of movements between the breeding and wintering distributions for Greater White-fronted Geese in East Asia. These sources suggest the existence of two biological flyway populations with contrasting population trends. The first consists of birds breeding on the Russian arctic, extending from the Khatanga River to east of Svyatoy Nos Cape (near Yana Bay, Yakutia), which migrates to winter in China where it is now almost totally confined to the Yangtze River floodplain. In recent years, this population has numbered between 30,000–55,000 individuals (compared to 140,000 in the 1990s), with > 70% concentrated at Poyang Lake in winter. The number of key sites identified for the species in China has increased with improved survey coverage since 2004. Birds from the second population also breed in arctic Russia, from east of Svyatoy Nos Cape to the Anadyr River, and winter in Japan and South Korea where 224,000–242,000 (in 2017/18 and 2018/19) and 178,000–182,000 (2018/19 and 2019/20) occur, respectively, compared to a total population size of 60,000 reported in the late 1990s. Although the telemetry studies provide single examples of tracked birds moving between the two populations, suggesting some permeability, we contend that the populations are relatively discrete, but recommend retaining three management units (for China-, Japan- and Korea-wintering birds) because of the count, management and legislative logic of doing so. The results given here provide a robust assessment of the current status of these populations, but between-year differences in count totals underline the need for continued improvement of the count system in China. They also build a stronger basis for the effective conservation for this species in the region, highlighting the need for improved monitoring and management for the declining numbers wintering in China.

Key words: biological flyway, distribution range, East Asia, China, Japan, South Korea, population trends.

The Greater White-fronted Goose *Anser albifrons* (hereafter GWFG) has an almost continuous circumpolar Arctic breeding distribution, wintering in temperate regions

of North America and Eurasia (Ely *et al.* 2005, 2017). Twelve populations are currently recognised globally (five for populations wintering in Europe, four in North America

and three in Far East Asia; Fox & Leafloor 2018), which are based on the migration routes and winter quarters of the different populations (Wetlands International 2019), determined through a combination of telemetry, ringing recoveries and genetic data (Wilson *et al.* 2018). Wetlands International has separated East Asian GWFG *A. a. frontalis* into three populations based on Chinese, Japanese and Korean wintering provenance (Ely *et al.* 2020) but, unlike delineation of the European and North American populations, we lacked firm evidence to support such distinctions in this region. Recent genetic evidence has confirmed that there were two GWFG populations in East Asia, based on mtDNA control region sequence data and microsatellite loci from samples taken on the summering grounds, which suggested that birds summering on the Lena River and Yana River were separate from those on the Kolyma River and Anadyr River (Wilson *et al.* 2018), while evidence from microsatellite loci DNA obtained from the wintering grounds confirmed that Chinese birds were genetically different from birds in Korea and Japan (Moriguchi 2019).

Moreover, whilst long-term count data showed that numbers wintering in Europe, North America, Korea and Japan are generally increasing (Fox & Leafloor 2018; Shimada *et al.* 2019), this was not the case for numbers wintering in China (Jia *et al.* 2016). In the last two decades, the wintering range of GWFG in China has contracted markedly from the coastal areas of Shandong and Jiangsu, resulting in the geese concentrating at their core inland wintering areas along the Yangtze River floodplain

since 1997 (Cao *et al.* 2008a, b). Subsequently, the species has disappeared from many wetlands in inland eastern China, so the majority now occur at the two largest lakes (Dongting and Poyang Lakes) on the Yangtze River (Cao *et al.* 2010). Hydrological changes caused by the Three Gorges Dam have reduced the availability of recession sedge meadows at East Dongting Lake (the main feeding habitat of Chinese-wintering GWFG), resulting in major declines in numbers wintering there in recent years (Zhao *et al.* 2012; Zou *et al.* 2017). However, the long-term decline in numbers wintering in China, contrasts with increasing numbers in Korea and Japan during 1988–2011 (Jia *et al.* 2016). From a management perspective, it is important to know how discrete these wintering populations are from each other – has loss and degradation of winter habitat in China (An *et al.* 2007; Xu *et al.* 2019) simply shifted GWFG to Korea and/or Japan? Or are these truly separate biological entities responding to different conditions prevailing in their respective flyways? In this analysis, we attempt to update and confirm the population trends for GWFG wintering in East Asia on the basis of flyway structure, by describing connections between the breeding, moulting, staging and wintering areas used by telemetry-tracked individuals.

Tracking of European GWFG showed that birds summering in Taimyr Peninsula migrated to central and western Europe (Kölzsch *et al.* 2016, 2019), supporting the suggestion that the Khatanga River marks the biogeographical watershed between GWFG wintering in the western and eastern Palearctic regions (Mooij & Zöckler 2000). Previous telemetry studies have shown

that Chinese (Yangtze) wintering GWFG ($n = 15$) summered between Khatanga Bay and Yana Bay in the eastern Russian arctic (Si *et al.* 2018; Deng *et al.* 2019). In contrast, Japanese-wintering GWFG ($n = 4$) summered in Chukotka, Russia (Takekawa *et al.* 2010) and Korean GWFG ($n = 6$) summered in the Sakha (Yakutia) Republic and Chukotka (Cheon *et al.* 2018), well to the east of the summering areas of Chinese-wintering geese. While these studies provided some evidence for flyway population structure among the East Asian GWFG, sample sizes and geographical distributions were too limited to confirm boundaries between discrete flyways within East Asia.

This study therefore integrates new and previously published telemetry data with wintering waterbird surveys and expert knowledge, to update our understanding of the breeding and wintering distribution of East Asian GWFG, to identify flyway populations, assess their current status and provide a stronger basis for the effective conservation for this species, especially for those declining numbers wintering in China.

Methods

Migration data

Migration routes were described by combining tracking data from GWFG in East Asia with expert knowledge, and the results used to describe populations in the region. Fifty flightless moulting adult or growing juvenile GWFG (11 adults: one male, one female and nine of unknown sex; 39 juveniles: 11 males, four females and 24 of unknown sex) were captured on the major breeding sites at Chaun Delta ($68^{\circ}53'N$, $170^{\circ}58'E$) and

Indigirka Delta ($70^{\circ}45'N$, $151^{\circ}28'E$) in Russia in 2017 and 2018. A further 68 GWFG were caught on the wintering ground in China (33 adults: 11 males, three females and 19 of unknown sex; 23 juveniles: four males, four females and 15 of unknown sex; 12 birds of unknown age and sex). All were caught on key wintering sites at Poyang Lake ($29^{\circ}07'N$, $116^{\circ}16'E$) and the Anhui Lakes ($30^{\circ}54'N$, $117^{\circ}40'E$) between October and March, from 2015 to 2017. In Korea, 32 GWFG (not aged or sexed) were captured at Jianghua Bay ($37^{\circ}17'N$, $126^{\circ}46'E$) in January 2017. Geese were caught on the wintering grounds by spotting them in the beams of powerful lamps at night then using hand-nets to lift them into boats from the water, or alternatively by using heavy-duty mist-nets (designed for catching large birds) set at their roosts. Those caught during summer were rounded up when flightless during the annual moult, with boats used to corral them from the water into movable funnel nets and pens established on the shore.

Birds were fitted with several types of solar-powered tags (Druidtech, China, 35 g, mounted on neck bands; Hunan Global Messenger Technology Company, China, 26 g or 27 g, mounted using neck bands or backpacks; KoEco, South Korea, 72 g, using backpacks; Ornitela, Lithuania, 38 g, mounted on neck bands), which recorded GPS positions and transmitted data via the GSM mobile networks. The transmitters provided 87 ± 68 (mean \pm s.d., range = 6–223) GPS positions per day, contingent upon power supply (for further details see Supporting Materials Table S1). Data from individuals with at least one complete

spring or autumn migration were used in determining the migration routes. Movement data for the day immediately following capture, and also for the last day data before the birds died or lost contact, were excluded from all analyses in case their behaviour was aberrant during these periods.

Migration data published by earlier research programmes were also collected by searching Web of Science for relevant studies using the expression: (GPS OR Argos OR PTT OR CTT OR (satellite* AND (track* OR transmitter* OR telemetr*))) AND (“Greater White-fronted Goose” OR “greater white-fronted geese”). Locations and corresponding timestamps of individual migration movements presented in the figures and tables of a previously published study were extracted (*e.g.* four tracks described by Takekawa *et al.* 2000; see Supporting Materials Table S2 for details).

Distribution and migratory range

The summer and winter distributions of GWFG in Asia, plotted by BirdLife International and Handbook of the Birds of the World (2019), were mapped in ArcGIS 10.2. These distributions were recently reviewed and updated by the Handbook of the Birds of the World team, using published literature and other information sources up to and including 2017. We amended these maps by incorporating the newly published and more complete field survey results from Fox & Leafloor (2018), Shimada *et al.* (2019), Krechmar & Kondratyev (2006) and Litvin (2011), as well from our own compiled wintering counts and from information on the

winter/summer distribution derived from satellite tracking data (see *Methods* below), supplemented by information gained from experts on the species in the East Asia flyway. The compilation of expert knowledge was achieved through a workshop held during the “2nd International Symposium on Developing Effective Coordinated Monitoring of East Asian Waterbirds in the 21st Century” in Beijing, China, in October 2019, when 12 experts from five countries (Supporting Materials Table S3) discussed and contributed to the delineation of the migration range of the East Asian GWFG and the coordination of this analysis.

Abundance estimates and trends in three populations

GWFG in East Asia have been segregated into three population units, based on wintering provenance, namely China, South Korea and Japan (Wetlands International 2019). Historically, this makes much sense, because it is expedient to count them in different countries, and each country maintains their own domestic policy and legislation that applies to their conservation management, protection from hunting and safeguarding of sites used by the species.

In our assessment of the numbers and trends for Chinese-wintering GWFG, abundance data prior to 2011/12 were derived from Jia *et al.* (2016). These were supplemented in winters 2015/16 and 2017/18–2019/20 by synchronous Yangtze waterbird surveys undertaken during mid-December to early February, which are thought to have covered the vast majority of GWFG wintering in China (Cao *et al.* 2010; Jia *et al.* 2016).

The Korean Ministry of Environment and its associated institutes – the National Institute of Environmental Research (until 2007) and the National Institute of Biological Resources (since 2008) – have 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 coordinated two-day field counts are undertaken annually in mid- or late January by ornithologists, experienced birdwatchers and volunteers to estimate the distribution and abundance of wintering waterbirds in South Korea (Supporting Materials Table S4).

In Japan, the “*Annual Census on Waterfowl (Anatidae) Population*” has been conducted by the Ministry of the Environment, with the assistance of prefectural governments, in mid-winter (*c.* 15 January) each year since 1970 (Table S4). This nationwide survey covers all principal sites for swan, goose and duck species throughout the country during the non-breeding season (Ministry of the Environment of the Government of Japan 2019).

Estimates of GWFG abundance in each country were based on mean counts of wintering surveys in 2018/19 and 2019/20 for China (the most recent and best coverage available), and on the average annual counts from the most recent available five years in South Korea (2015/16–2019/20) and Japan (2014/15–2018/19). Simple linear regressions were taken as the default approach to the analysis of \log_{10} -transformed annual count data to detect the general trends for the three population units: Japan, China and South

Korea. However, temporal trends in counts of long-lived waterbirds may be temporally autocorrelated (*e.g.* Wood *et al.* 2019), and hence the regression assumption of independent errors may not be met. Initial assessments were therefore made of linear regression residuals of temporal trends in the count data of all three countries, fitted using the nlme package in R (Pinheiro *et al.* 2020; R Core Team 2020). Inspections of the resulting autocorrelation plots showed evidence of statistically significant ($P < 0.05$) residual temporal autocorrelation in the regression models for both South Korea and Japan, but not China. To assess the country-specific linear trends in counts, generalized least squares autoregressive models were fitted to allow for model errors to be correlated (Pinheiro *et al.* 2020). Autocorrelation structures were included in each model according to the years over which significant residual autocorrelation was detected; China = 0, South Korea = 1, and Japan = 4. Efron’s R^2 was used to quantify the goodness of fit of each model (Efron 1978), as this pseudo R^2 represents the explained variance and strength of correlation between actual and predicted values, and is thus analogous to true R^2 (which cannot be estimated for generalized least squares regression models with autocorrelation structures). For each model Efron’s R^2 was calculated as:

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

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

Key wintering sites in East Asia

In each country, key sites were determined from the count data recorded during 2015/16–2019/20, with those that exceeded 1% of the total estimated in any single year during this period considered to be of national importance for the species (Table 1). In addition, based on the population definitions arising from the results of the telemetry study, we identified sites of international importance based on Ramsar Convention Criterion 6, 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). These levels are also identified in Table 1.

We investigated changes in the number and distribution of GWFG at key sites in China over the past two decades by comparing annual maximum counts at these sites from 2003/04–2019/20 inclusive. In addition to the survey data described above, surveys of known key sites (Poyang Lake, Dongting Lake, Hubei and Anhui Lakes) along the Yangtze River floodplain in winters 2007/08–2014/15 and 2016/17

Table 1. Population size estimates for Greater White-fronted Goose in China, Japan and South Korea in different time periods, together with the current 1% criteria for determining sites of national and international importance for the species in East Asia (internationally important sites being those that regularly support $\geq 1\%$ of individuals in a population; Ramsar Convention Secretariat 2010). Flyway criteria are based on geese wintering in China following a different flyway to those wintering in South Korea and Japan.

| Timing of population estimate | China | South Korea | Japan |
|----------------------------------|----------------------|----------------------|----------------------|
| Population estimate in the 1990s | 142,000 ^a | 61,328 ^a | 28,300 ^a |
| Population estimate in 2005 | 33,000 ^b | 30,275 ^b | 69,732 ^b |
| Population estimate in 2011 | 18,000 ^c | 85,000 ^c | 192,500 ^c |
| Population estimate in 2020 | 48,000 ^d | 123,500 ^e | 204,000 ^f |
| 1% national criteria | 480 ^g | 1,235 ^g | 2,040 ^g |
| 1% flyway criteria | 480 | 3,275 | 3,275 |

Notes: ^apopulation estimate in the 1990s is based on mean wintering count number from 1990–1999; ^bdata from Cao *et al.* (2008); ^cdata from Jia *et al.* (2016); ^dpopulation estimate in 2020 is based on a mean of the maximum numbers counted each winter during 2018/19–2019/20; ^epopulation estimate in 2020 is based on a mean of the maximum numbers counted each winter during 2015/16–2019/20; ^fpopulation estimate in 2020 is based on a mean of the maximum numbers counted each winter during 2013/14–2018/19; ^gnew 1% criterion based on new population estimates of each unit.

were also included (Supporting Materials Table S5).

Results

Summer range

Combining all sources of information showed that GWFG in East Asia summered mainly in the Russian arctic and sub-arctic tundra, along the Arctic Ocean coast between Khatanga Bay (73°7'N, 106°18'E) and the Bering Sea coast (63°24'N, 178°45'E; Fig. 1). Expert opinion and telemetry results suggest that the GWFG summering in the lower Anadyr River on the Bering Sea coast (64°10'N, 177°5'E) and in other parts of eastern Chukotka are somewhat isolated from the arctic coastal population which otherwise extends more or less continuously westwards from Chaun Delta (Fig. 1). A small and fully isolated enclave is known to exist in the boreal forest in the Kava River basin on the Sea of Okhotsk coast (59°40'N, 147°20'E; Fig. 1) and there remains the possibility that more such groups occur in the taiga forest, which are currently undocumented. Our assessment of GWFG distribution in East Asia (Fig. 1), differs from the ranges given in the BirdLife International and Handbook of the Birds of the World (2019) in that tagged GWFG generally avoided taiga forest (excepting the isolated group on the northern coast of the Sea of Okhotsk) and mountain landscapes, with activity concentrated in the tundra biome during the summer. Following expert opinion, and invoking the precautionary principle, we have retained shading for the Chukchi Sea coast tundra between the Chaun Delta and the Bering Strait despite

the absence of telemetry data for this area, in anticipation of further data to make a more rigorous assessment of the eastwards distribution becoming available in the future.

Winter range

Chinese count data show that GWFG no longer winter along the coast of Shandong and Jiangsu Provinces, but have become concentrated at four wetlands (East Dongting, Poyang, Shengjin and Caizi Lakes) along the Yangtze River floodplain (Cao *et al.* 2008a,b; see Supporting Materials Table S6). This suggests a contraction of range compared to their broader distribution in earlier surveys (Cao *et al.* 2010; Zhao *et al.* 2012). Consistent with Jia *et al.* (2016) and Shimada *et al.* (2019), Japanese GWFG continue to be mostly concentrated in Miyagi Prefecture, with relatively small numbers in southern Japan, while South Korean geese are still widely distributed along southern and western coasts and in the northern plains of South Korea. Despite the increase in wintering numbers in Japan and Korea, and the maintenance of range in these countries, the more recent information from China implies a genuine retraction in distribution there (Fig. 1).

Defining two biological flyway populations in East Asia

The telemetry data delineated two, almost completely distinct, GWFG flyways in East Asia. The first (which we recommend designating the “East Asia Continental Population”), consisted of Siberia-breeding birds which almost exclusively travelled to wintering areas in China (Fig. 2). Geese that bred in far-eastern arctic Russia formed a

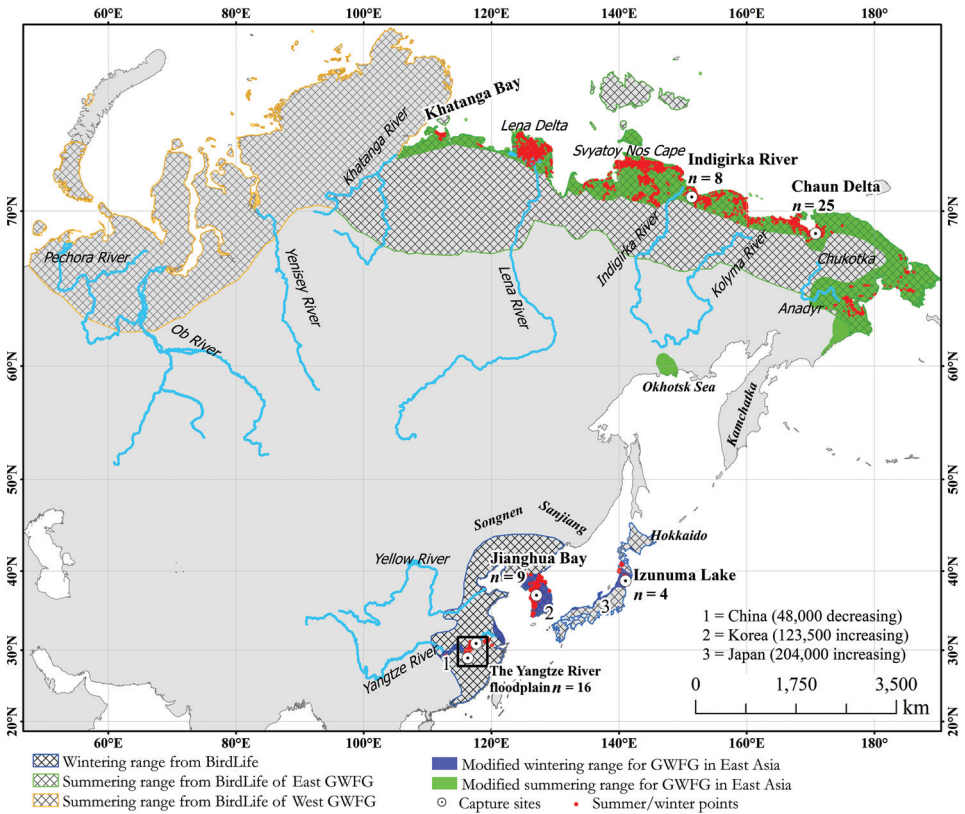


Figure 1. Revised distribution map of the Greater White-fronted Goose in East Asia, modified from BirdLife International and Handbook of the Birds of the World (2019). Summer distribution (shaded in green) ranges from Khatanga Bay to the south of the Anadyr River and an enclave adjacent to the Okhotsk Sea. Winter distribution (shaded in blue) extends along the Yangtze River floodplain in China, the northeast and western coast of Japan, and the southern and western coast and the northern plains of South Korea. Information for the revised summering range was based on tracking data (red points, which represent GPS locations for each individual point between arrival and departure in summer; see Fig. 2), expert knowledge and a literature review which included reports from Fox & Leafloor (2018), Krechmar & Kondratyev (2006) and Litvin (2011). The revised wintering range was based on field survey data, expert knowledge (see *Methods* for details) and information from the literature (Fox & Leafloor 2018; Shimada *et al.* 2019). One hundred and fifty-four individuals were caught in two key areas (including on the Chaun Delta and Indigirka Delta) within the summering range, and at three key wintering areas (the Yangtze River floodplain, Jianghua Bay and Izunuma Lake) to validate and supplement expert knowledge of the species in East Asia. Circles with black dots = capture sites; *n* = the number of birds that completed at least one spring or autumn migration, in total 62 individuals. All site/area names mentioned in the paper are indicated on the map. Population sizes and trends are results from this study, based on count data from winter surveys in China (1992/93–2019/20) and Japan (January 1970–2019).

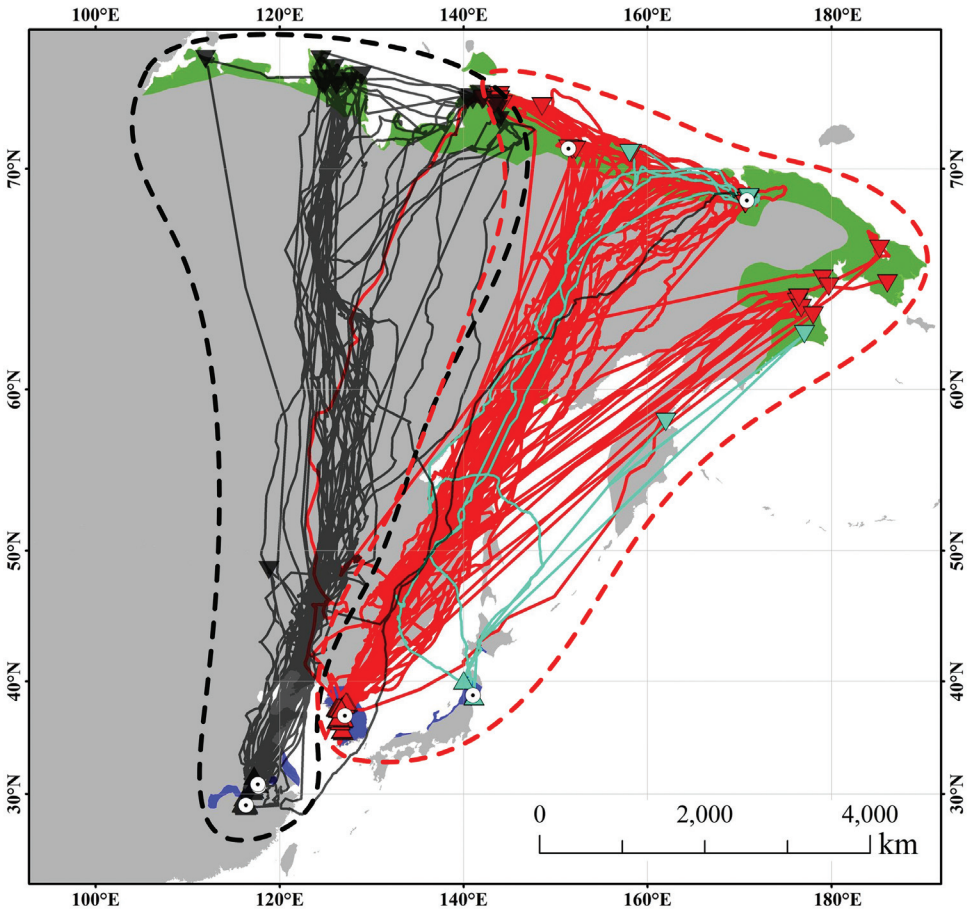


Figure 2. Ranges of two distinctive Greater White-fronted Goose flyways in East Asia: 1) the East Asian Continental Population (black dashed line), and 2) the West Pacific Population (red dashed line). East Asian Continental Population birds wintering in China migrated to summering sites between Khatanga River and Svyatoy Nos Cape. In the West Pacific Population, geese which summered near the Indigirka River and in Chaun wintered in South Korea and Japan, geese wintering in South Korea summered in Svyatoy Nos Cape and Chukotka, whilst geese wintering in Japan summered in Anadyr). These definitions are based on migration routes of 62 geese tagged on five main summering/wintering area crossed their distribution range (circles with black dots indicate capture sites), including 17 in China (black solid lines), and 45 in Korea, Japan and Russia (red and light blue solid lines; four were extracted from Takekawa *et al.* (2000)). Light green shaded areas indicate our revised suggestion for the summering range; dark blue areas represent that for the revised wintering range. Inverted and regular triangles show the summering and wintering areas used by tracked individual(s).

second, separate group of birds (which we suggest calling the “West Pacific Population”) which migrated to winter quarters in Korea and Japan (Fig. 2).

The East Asian Continental Population was described by 17 individuals whose tags provided full migration data, including 22 autumn tracks and 23 spring tracks. The birds were all caught in China on the Yangtze River floodplain, summered between the Khatanga River and Svyatoy Nos Cape (72°52'N, 141°01'E), and migrated over the Russian taiga forest and across the Songnen Plain of northeast China to their wintering sites. These geese wintered mainly at Poyang Lake, Dongting Lake and Anhui lakes in the middle and lower Yangtze River in China (Fig. 2).

The West Pacific Population was described by the GPS locations from 45 individuals, whose tags provided full migration data, including 48 autumn tracks and 20 spring tracks. Thirty-two geese were captured in the Chaun Delta and the lower reaches of the Indigirka River, all moulted to the east of Svyatoy Nos Cape, migrated along the Kolyma-Okhotsk corridor, the lower Amur River and the Sanjiang Plain of Northeast China, and wintered in South Korea and Japan. Nine and four birds were captured on the wintering grounds in South Korea and Japan, respectively. They also staged in the Sanjiang Plain of northeast China, and then summered from the Indigirka River east to the Anadyr River. Birds that wintered in Japan and South Korea showed considerable overlap in summering and staging areas, strongly suggesting that, despite separate winter quarters, these birds belong to the same population (Fig. 2).

Despite most flight-lines for the GPS-tagged geese indicating almost complete separation of these two population migration routes, they were not completely isolated from each other. A very few individuals crossed between these putative flyways during their annual life-cycle, showing some degree of permeability. For instance, gwfg035 (a juvenile male) hatched in the Chaun Delta, staged on the Sanjiang Plain *en route* to winter along the Yangtze, China. The route taken was that of the West Pacific Population, whereas its wintering site belongs firmly in the East Asian Continental Population. In addition, gwfg028 (juvenile) hatched in the Chaun Delta, staged in the Songnen Plain in its second autumn, which is a staging area of the East Asian Continental Population, but nevertheless wintered and summered in the West Pacific Population.

Some GWFG from both flyways also shared a moulting site in the eastern part of Svyatoy Nos Cape, which was used by some moulting non-breeders and unsuccessful breeders from the Lena Delta as well as by some Chaun-hatched GWFG from the West Pacific population in their second year.

Population size and trends of wintering populations

Long-term count data for GWFG in Japan and South Korea show increasing numbers wintering in both countries (Fig. 3; Supporting Materials Table S4). From 1969/70 to 1984/85, Japanese counts ranged from 3,000–5,000 birds (Fig. 3), but have maintained steady growth since 1984/85 (Table 2). By the winter of 2018/19, numbers of GWFG counted in Japan had reached 241,149, an increase of 60-fold

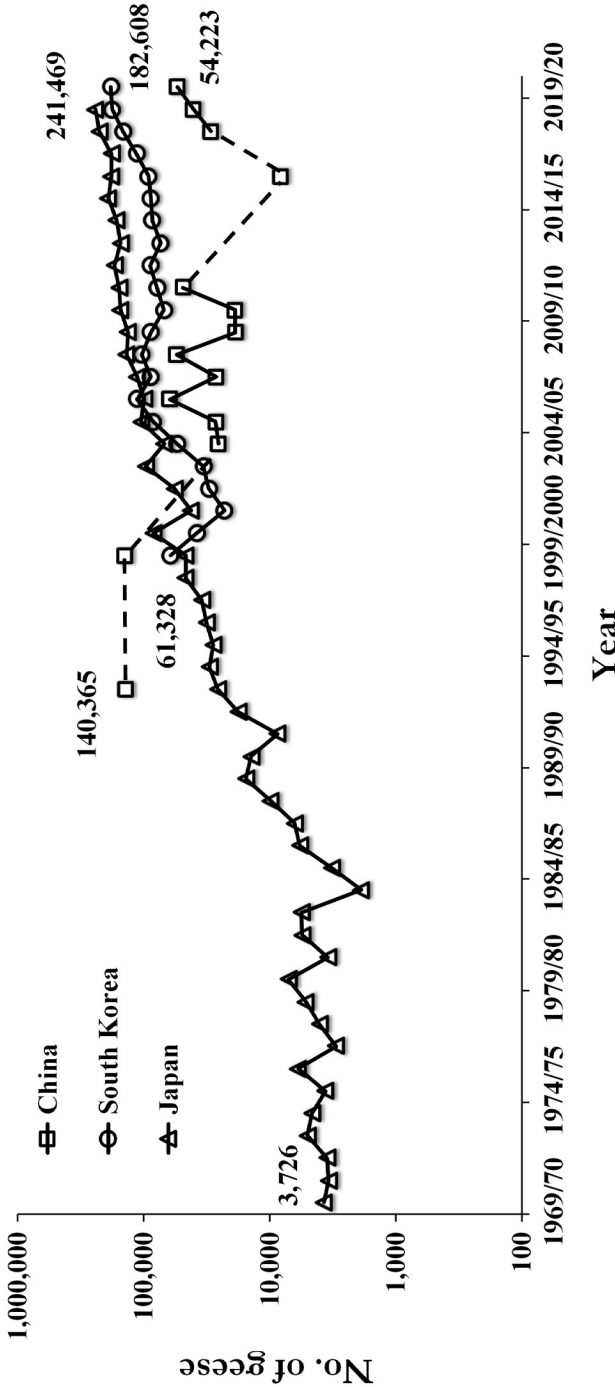


Figure 3. Abundance estimates and trends in wintering numbers of Greater White-fronted Geese counted in the three management units (China, South Korea and Japan) during 1969/70–2019/20. Numbers estimated for Japan and South Korea are derived from wintering surveys in 1969/70–2018/19. Numbers estimated for China during 1992/93–2010/11 were obtained from Jia *et al.* (2016); those from 2011/12–2019/20 were based on winter surveys. National count totals for the earliest and latest year of available wintering surveys in each country are shown (see Supporting Materials Table S4 for more details). Dashed lines connect counts with interim missing count data in the corresponding years.

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

| Country | ACS | Parameter | Estimate | s.e. | <i>t</i> value | <i>P</i> value | Efron's <i>R</i> ² |
|----------|-----|-----------|----------|--------|----------------|----------------|-------------------------------|
| China | 0 | Intercept | 50.753 | 21.680 | 2.341 | 0.037 | – |
| | | Year | –0.023 | 0.011 | –2.130 | 0.055 | 0.274 |
| S. Korea | 1 | Intercept | –51.839 | 11.518 | –4.500 | < 0.001 | – |
| | | Year | 0.028 | 0.006 | 4.925 | < 0.001 | 0.646 |
| Japan | 4 | Intercept | –82.226 | 6.767 | –12.152 | < 0.001 | – |
| | | Year | 0.043 | 0.003 | 12.802 | < 0.001 | 0.928 |

since the 1970s. Wintering numbers in South Korea also showed an overall increase since 1998/99 (Table 2), although numbers dropped sharply to 22,817 in 1999/2000 before increasing again to stabilise at around 80,000–90,000 between 2001/02 and 2015/16. Subsequently, numbers had reached 182,608 by 2019/20, approximately triple the number in the late 1990s (Fig. 3). In contrast, numbers counted in China have shown long-term declines since 1998/99, although this decline was not statistically significant for the entire time-series (Table 2). From a total of 142,159 counted in 1992/93, numbers fell to 8,190 in 2015/16 (6% of the previous highest count), although numbers have recovered slightly in recent years, reaching 54,223 in 2019/20. Increases in China in very recent years may reflect improved count coverage rather than genuine increases in abundance (see *Discussion* below).

Key wintering sites in China, South Korea and Japan

In China, four key wintering sites for GWFG were identified from the count

data: East Dongting Lake, Poyang Lake, Shengjin Lake and Caizi Lake, all within the Yangtze River floodplain and all of international importance (Supporting Materials Table S5). Thirty-five key wintering sites for GWFG were identified in South Korea, widely distributed along the south and west coasts, with others in the northern plain; twenty of these sites have supported internationally important numbers of GWFG in winter (Table S5). Six key wintering sites were identified for GWFG in Japan, mostly in Miyagi Prefecture, including Lake Izunuma, Lake Kabukurinuma and Lake Kejonuma, where most of the Japanese GWFG wintered, and four of these sites qualified as being of international importance for GWFG (Table S5, Fig. 4).

Changes in numbers of Chinese GWFG at key wintering sites

Four of the most important key wintering sites of GWFG in the Yangtze River floodplain (Poyang, East Dongting, Shengjin and Caizi Lakes) have been monitored

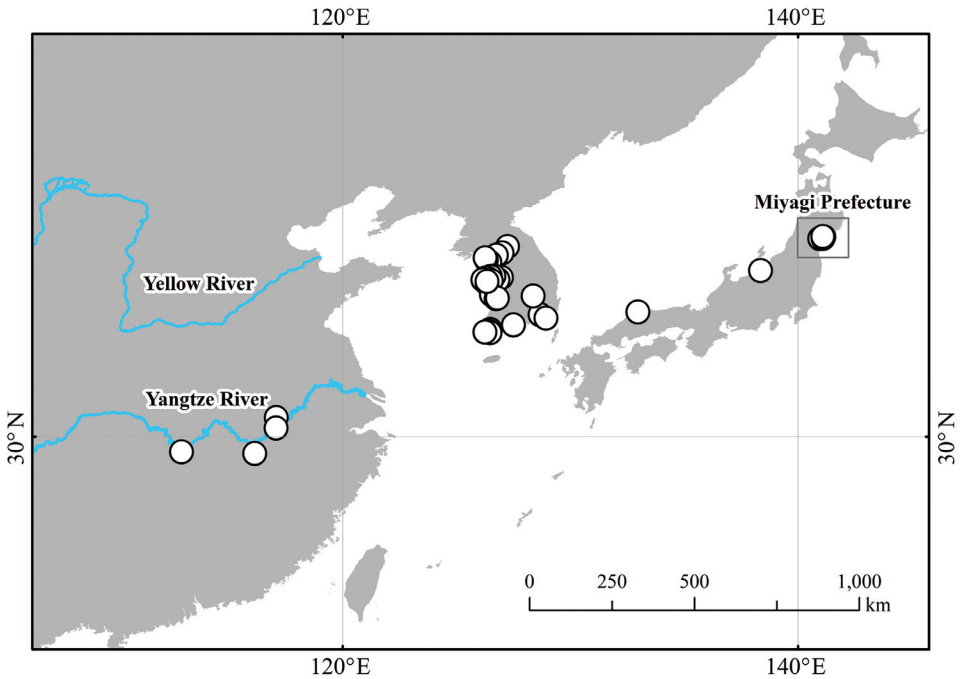


Figure 4. Sites of national importance (white circles) for Greater White-fronted Geese wintering in Chinese, South Korean and Japanese management units, based on the maximum numbers counted at each site during surveys carried out in winters 2015/16–2019/20 (1% threshold = 480 birds for China, 1,235 for South Korea and 2,040 for Japan).

regularly during winter from 2003/04 until 2019/20 (Supporting Materials Table S6). The number of GWFG in these lakes changed significantly after 2009. The overall trend is that birds shifted from the middle to the lower reaches of the Yangtze River, with numbers increasingly concentrated at Poyang Lake (Fig. 5). Numbers of GWFG counted in winter at East Dongting Lake have declined markedly, from about 13,000 birds present in 2003/04 compared to < 100 individuals in 2008/09, although numbers have since partially recovered to 5,124 individuals in 2019/20. Whilst Poyang Lake (Jiangxi Province) has always been one of

the main wintering sites for GWFG, with 15,000 birds counted (scattered around the shores of the lake) in 2004/05, numbers more than doubled to 40,627 birds in January 2020, albeit that now most GWFG concentrate in the centre of the lake (Fig. 6), which may affect their detectability during the survey. There were only 90 GWFG wintering at Shengjin Lake in 2004/05, but in more recent years numbers wintering on this lake have stabilised at 5,000–6,000 birds. Likewise, there were almost no GWFG at Caizi Lake in 2004/05, but numbers there increased to > 2,000 during winter 2019/20.

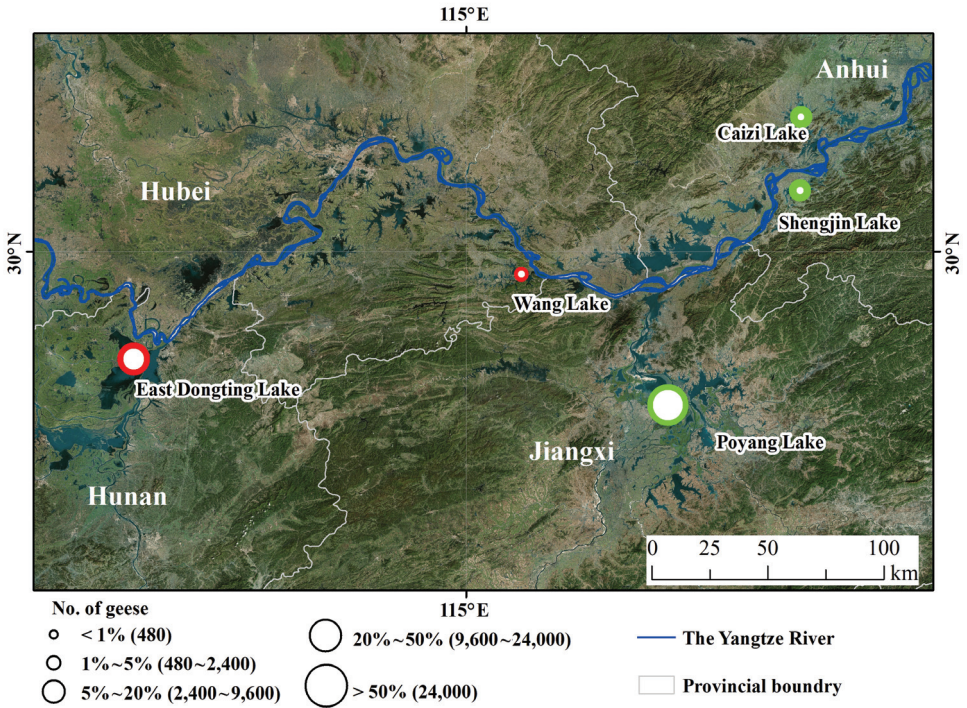


Figure 5. Relative percentage changes in the numbers of wintering Greater White-fronted Geese counted at five key wintering sites in China before 2010 compared with counts after that year. Green circles show sites with increasing numbers and red circles are those with decreasing numbers. Circle sizes represent different orders of magnitude, as shown in the key.

Discussion

Summer and winter distribution of East Asian GWFG

For the first time, we integrated satellite tracking data, survey data and expert opinions to summarise our understanding of the breeding and wintering distribution range and population structure of the Greater White-fronted Goose in East Asia. The results showed that GWFG mainly breed in the arctic tundra area between Khatanga Bay and the lower reaches of the Anadyr River (consistent with Mooij &

Zöckler 2000), supporting the assertion that Khatanga River is the geographic boundary between western and eastern Palearctic populations. The distribution of the tracked birds and expert knowledge also resulted in the summer range of the species generally being realigned northwards, but also extending south along the coast at the easternmost edge of the range (Fig. 1). We should however be highly prudent in concluding too much from the results of what remain a restricted sample of GPS-tagged birds. We know, for example, that there is at least one isolated group of

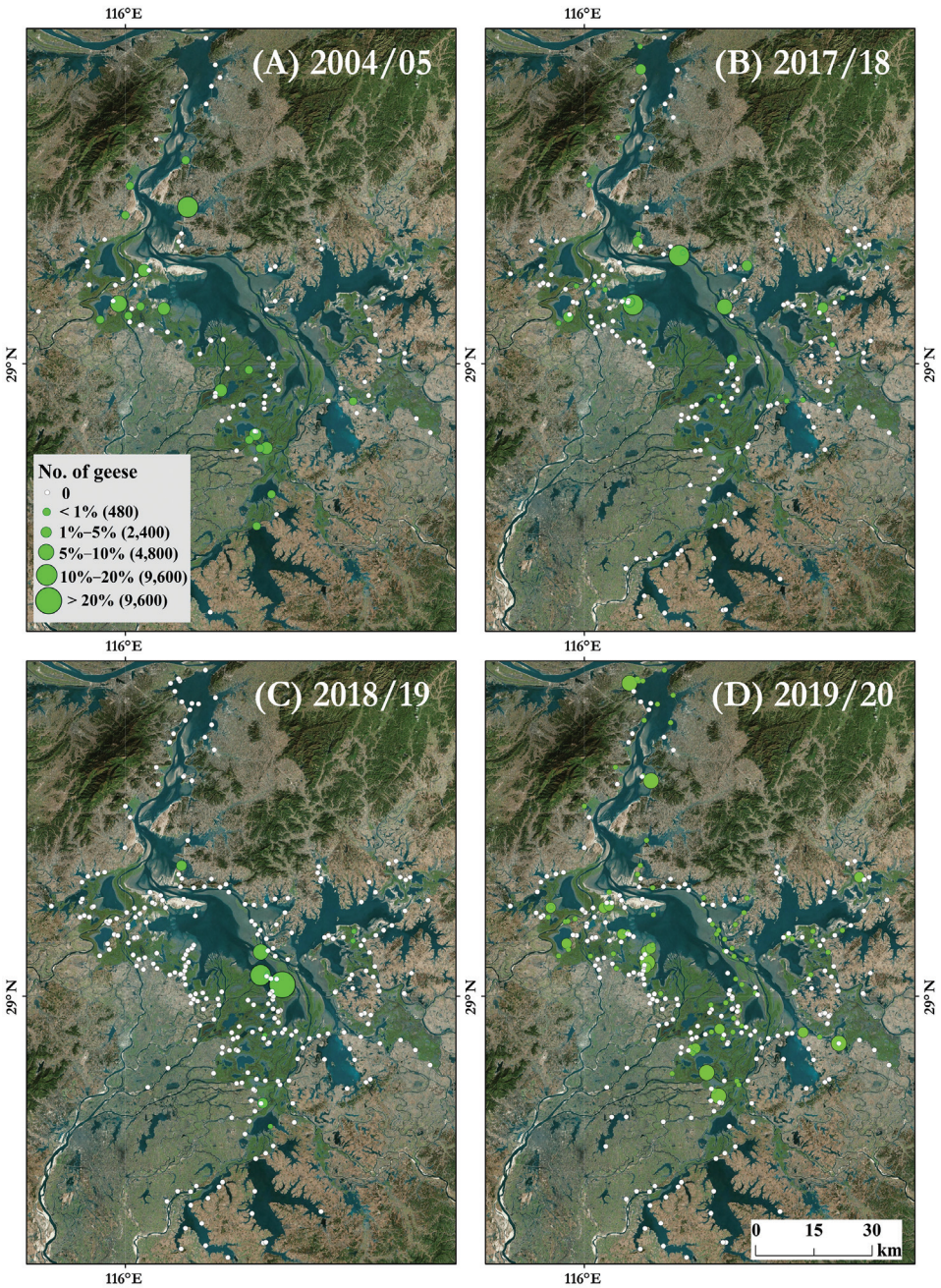


Figure 6. Distribution of Greater White-fronted Goose within Poyang Lake, China, in 2005, 2018, 2019 and 2020. Circle sizes indicate numbers counted as a proportion of the total population estimate for China.

GWFG that breed in the taiga along the northern coast of the Okhotsk Sea, and historical accounts from Russia suggest that more may exist (Krechmar & Kondratyev 2006; Litvin 2011). By catching geese in the arctic tundra biome and at major wintering sites, the sample of marked birds is biased, due to our restricted access to catch sites, towards particular areas regularly used by geese during their annual cycle. Apart from a single aerial survey by Hodges & Eldridge (2001), there is a lack of comprehensive GWFG distributional data from the Russian arctic during the breeding season. Furthermore, the lack of comprehensive knowledge of the GWFG breeding outside of the tundra region restricts our ability to map accurately the true summering range of GWFG in the taiga biome. Hence, while we consider that our modified distribution maps represent progress, we acknowledge that accurate mapping of the GWFG summer range awaits systematic waterbird surveys (*i.e.* aerial surveys at least once in 10 years) to determine their breeding and moulting distribution in the taiga zone. These are required to establish a more detailed picture of the range of this important species in the arctic.

Two biological flyway populations in East Asia

The results of the telemetry studies support the genetic identification of two separate biological flyway populations for GWFG in East Asia: an East Asian Continental population and a West Pacific population. Although suspected previously, this evidence based on movements of individual birds is the first to confirm that this is largely the

case, albeit with occasional movements of single individuals between populations in either direction. GWFG tracked from China summered mainly between Khatanga River and Svyatoy Nos Cape, with major breeding populations existing in the Lena Delta and Yana Delta, consistent with previous studies (Fox & Leafloor 2018; Si *et al.* 2018; Deng *et al.* 2019). However, of the geese tracked from South Korea, two-thirds migrated to Chukotka, which was formerly considered to be the breeding grounds primarily for Japanese GWFG. Furthermore, a bird that wintered in Miyagi Prefecture, Japan, bred in the Chaun Delta and moulted in the Kolyma Estuary for two years, where Korean birds were typically thought to summer. Previous studies had already revealed that Japanese- and Korean-wintering GWFG overlapped in their staging areas and potentially at breeding and moulting sites. Yamaguchi & Higuchi (2008) found that GWFG wintering in Sanin, located in the western part of Japan, flew directly over the Sea of Japan to the Korean Peninsula during spring migration, before migrating through northeast China together with Korean-wintering geese. Gwfg017 captured in South Korea, migrated through the Kamchatka Peninsula, and staged in Hokkaido for more than 40 days during autumn migration, before it finally wintered in South Korea. In addition, birds marked in South Korea were found in Hokkaido and Miyagi Prefecture during winter (C.Y. Choi, unpubl. data). The combination of recent and historical telemetry data suggests that, while there is a considerable degree of exchange between Japanese- and Korean-wintering GWFG throughout the annual cycle, these birds

interact far less with GWFG wintering in China. This assertion is further supported by the analysis of the genetic structure of GWFG wintering in Japan, Korea and China. This work suggested that East Asian GWFG wintering in China were genetically distinct from those wintering in Japan and South Korea, which differed little in genotype (Moriguchi 2019) confirming genetic exchange between birds wintering in Japan and Korea, which interacted less with those wintering in China. We therefore recommend that, until more information is forthcoming, the East Asian GWFG should be considered as consisting of two discrete populations, although there is no doubt that it is expedient to monitor and manage them in three separate nations (China, Korea and Japan), reflecting the ease of monitoring, managing and legislating for such a migratory species within the domestic legislative frameworks, with emphasis upon South Korea and Japan working closely together to protect and manage their shared population.

Abundance and trends amongst wintering population units

Our combined count data provided updated winter abundance estimates and population trends from 2011/12 to 2018/19 (for Japan) or 2019/20 (for China and South Korea). There have been no clear trends numbers of GWFG wintering in China since the 1990s, although generally numbers since 2000 have been one-third of those counted in the 1990s. What is more marked is the contraction of the range, which apparently has occurred since the early 2000s. Although the total numbers of GWFG counted

wintering in China has increased since the early 2000s, we cautiously emphasise that this could be due to improved waterbirds survey coverage in the Yangtze River floodplain in recent years (Supporting Materials Table S7). For example, the most recent (2018/19 and 2019/20) survey of Poyang Lake covered the centre of the lake more effectively than in the past, and many more birds were counted in this part of the lake (Table 1 and Fig. 6), amounting to 79% and 75% of the total numbers recorded in China in 2019 and 2020, respectively. Unlike the annual systematic surveys of South Korea and Japan, only four systematic surveys of China have been conducted since 2012. During 2011/12 to 2014/15 and in 2016/17, wintering surveys only covered a portion of the key wetlands in the Yangtze River floodplain, making it hard to estimate the true abundance and trends of GWFG wintering in China in these years. The establishment of a continuous, standardised waterbird monitoring system in China would greatly enhance our ability to obtain a better estimate of total population size and to detect the trends in site, regional and national abundance for GWFG in China.

Numbers of GWFG wintering in South Korea recently stabilised at around 80,000–90,000 birds (Jia *et al.* 2016), although showing a significant increasing trend overall. Dense single-species crops (such as rotational grassland, early growth cereals and root crops), as well as spilled grain post-harvest in agricultural landscapes, have been found to provide geese with higher quality food (enhancing their calorific and nutritional intake) than vegetation in natural

or semi-natural habitats (Fox *et al.* 2017). It is therefore highly likely that increasing numbers of wintering GWFG in South Korea have benefitted from the increase in availability of spilled rice left after the harvest in areas that were formerly intertidal mudflats and saltmarshes, which have been embanked, drained and converted into rice paddies (Fujioka *et al.* 2011; Kim *et al.* 2016). These areas often are also situated in close proximity to safe night-time roosts on wetlands and open water, which make them ideal as foraging areas (Fujioka *et al.* 2011).

Japan holds the largest proportion of GWFG wintering in East Asia (Shimada *et al.* 2019) and overall numbers wintering there are increasing, although numbers in the south and north (98.7% in 2018/19) of the country showed contrasting trends. Shimada *et al.* (2019) found that > 80% of all Japanese GWFG were concentrated in Miyagi, where numbers have continuously increased, while their abundance in Hokuriku and Sanin have decreased year by year. It has been speculated that the combination of crops available in northeast Japan has been the major attraction to GWFG there (Shimada & Mizota 2011), and Moriguchi *et al.* (2013) has already demonstrated that the distribution of rice fields is an important factor influencing GWFG distribution in Japan. A warming climate may also have contributed to fundamental shifts in the distribution and abundance of GWFG (Shimada *et al.* 2005). Japanese GWFG wintering in different regions may originate from different breeding areas, as suggested by differences in migration routes based on telemetry results (Yamaguchi & Higuchi 2008; Fox &

Leafloor 2018), so differential survival and reproductive success related to these differences could additionally affect local wintering abundance. Further telemetry studies of GWFG from different wintering areas of Japan would help to illustrate the challenges faced by individual geese throughout the annual life-cycle along each route, to identify potential reasons for the different trends in each region.

The period of declining abundance in the Chinese GWFG population was coincident with the increase in South Korea and Japan, so we cannot rule out the possibility that Chinese birds simply moved to Korea or Japan. However, the results of analysis of microsatellite DNA of Moriguchi (2019) from China and Japan help to rule out this possibility as an explanation. Both Japanese- and Korean-wintering groups overlap on their breeding areas in Chukotka, where recent climate warming allows prolonged, highly productive vegetation growth, providing plentiful food to large herbivorous birds (Solovyeva *et al.* 2019) as supported by local increases in breeding abundance of GWFG nesting in the Chaun-Delta since 2016 (D. Solovyeva, *in litt.*). Although lying well north of the 0°C mean January isotherm, North Korea remains also a potential wintering area for the species, but we know very little about the status of waterbirds in that country; it would be extremely useful to know more about the status of the GWFG there.

Key GWFG wintering sites in the three countries

Since the analysis of Jia *et al.* (2016), the number of key wintering sites for GWFG in

Japan increased to six in 2015/16, although all of the new key sites are concentrated in Miyagi Prefecture in northern Japan. The increase in the number of key GWFG wintering sites in northern Japan may be linked to dispersal from traditional areas caused by increasing numbers in the population as a whole dispersing to other wintering areas. Alternatively, the area of suitable crops may have reached the point where more habitat is available to support geese than previously. Although a previous study showed that rice cultivation was a major factor influencing the distribution of GWFG in Japan (Moriguchi *et al.* 2013), this may not currently be the case. Establishing the causes of the increase in number of key sites requires further analysis of habitat selection by GWFG in Japan through satellite tracking, remote sensing data and agriculture statistics.

With the significant increase in numbers of GWFG wintering in South Korea, the number of key sites there has decreased from 37 to 35 locations, despite the loss of natural wetlands in southern and western Korea, which no longer attained key site status. It has been speculated that the GWFG at these sites may have moved to nearby sites closer to farmland (Fujioka *et al.* 2011; Kim *et al.* 2016), although this again requires confirmation by undertaking habitat selection studies during the wintering period to compare with the historical situation.

Since 2008/09, new key wintering sites have been identified for GWFG in China, with internationally important numbers now occurring at Shengjin Lake and Caizi Lake in Anhui Province. East Dongting Lake was formerly a key GWFG wintering site,

supporting thousands of geese in the 1990s, but only a few hundred individuals have been counted there in the last ten years. This is thought to be mainly due to local loss of sedge *Carex* sp. and associated habitat change at this site caused by hydrological changes related to Three Gorges Dam (Zhao *et al.* 2012). The rise in numbers at Shengjin and Caizi Lakes may be a result of management measures adopted by the local government and national nature reserve authorities, including restoring former farmland to natural habitat and banning fishing across the entire lakes. Farmland restoration has accelerated at Caizi Lake since the late 1990s, with soil hydrology and the extent of natural wetland vegetation improving significantly since that time (Bao *et al.* 2016; Gen *et al.* 2017), factors that are likely to have contributed to the increase in numbers of wintering waterbirds (including GWFG) at the site. Winter water level recession now exposes extensive graminoid meadows in the northern and southern parts of Caizi Lake favoured by GWFG (Zhou *et al.* 2019), consistent with their observed redistribution and increase in abundance in the area. Peak numbers of GWFG at Shengjin Lake appear in the early and late wintering period, and tracking data for individual GWFG showed that many birds leave the site for Poyang Lake in mid-winter. Zhao *et al.* (2012) showed that water levels directly affected the distribution of GWFG, but seasonal water levels at Shengjin Lake formerly were controlled artificially by fishing interests. Now that fishing is banned and greater emphasis placed on biodiversity conservation at the site, it may be possible to control water

levels in a way that is more sympathetic to providing sedge meadows in a form that is attractive to GWFG at the site throughout the entire winter. Tracking data also showed that some GWFG moved from Poyang Lake back to Shengjin Lake in late winter, prior to their spring migration. Further research, combining telemetry with studies of food quality and availability, might be useful in explaining the causes of such within-winter between-sites shifts made by birds, and thus indicate how sympathetic management may enhance the current carrying capacity of available habitats.

Finally, we know very little about the relative contribution of goose hunting in Russia to the dynamics of geese from the two populations. The migration season is the traditional hunting season in Russia and many birds are hunted annually (L. Cao, unpubl. data) so, in the absence of metal ring recoveries, telemetry offers another mechanism for monitoring the level of hunting at specific sites.

Conservation and research recommendations

Establishment of a coordinated long-term continuous and standardised monitoring programme on the winter quarters (especially in China) would help to describe changes over time in species abundance at a suite of key sites and at the population level, for informing the management of GWFG locally, regionally and across East Asia. Closer collaboration between monitoring, research and management interests should combine telemetry data with within-site distributional count data to investigate the causes of between-site movements in

relation to food profitability and availability, in order to guide and improve habitat management programmes. These monitoring data will help towards developing targeted conservation strategies at the site, regional and population levels for this species.

We believe that more extensive telemetry studies will continue to identify important habitats and conservation gaps for GWFG in East Asia and potentially enlighten future responses to climate change. GWFG wintering in Japan and South Korea have moved from natural wetlands to farmland to forage in the last 50 years (Fujioka *et al.* 2011; Kim *et al.* 2016), which may have contributed to the significant increase in abundance in these areas. It has been suggested that food provision on agricultural land in China could in the same way contribute to restoring GWFG abundance there, although this will need some management and potentially mitigation measures for farmers to remove the currently adverse conditions for geese there at present, perhaps by providing sacrificial grain on stubble fields, or by tolerating goose grazing of winter and spring cereals (Zhao *et al.* 2018).

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References

- An, S., Li, H., Guan, B., Zhou, C., Wang, Z., Deng, Z., Zhi, Y., Liu, Y., Xu, C., Fang, S., Jiang, J., Li, H. 2007. China's natural wetlands: past problems, current status, and future challenges. *Ambio* 36: 335–342.
- Bao, X., Cheng, X., Ji, L., Zheng, Z., Kong, L. & Zhang, P. 2016. Characteristics of soil enzyme activities in wetlands with various restoration ages in Caizi Lake, Anhui Province. *Soils* 48: 692–697.
- BirdLife International and Handbook of the Birds of the World. 2019. *Bird Species Distribution Maps of the World*. Version 2019.1. BirdLife International, Cambridge, UK. Available at <http://datazone.birdlife.org/species/requestdis> (last accessed 28 December 2019).
- Cao, L., Barter, M., Lei, G. & Yang, Q. 2008a. Anatidae in the Yangtze Floodplain in winter 2004 and 2005. *Casarca* 11: 146–160.
- Cao, L., Wang, X., Wang, Q. & Barter, M. 2008b. Wintering Anatidae in China: a preliminary analysis. *Casarca* 11: 161–180.
- Cao, L., Zhang, Y., Barter, M. & Lei, G. 2010. Anatidae in eastern China during the non-breeding season: geographical distributions and protection status. *Biological Conservation* 143: 650–659.
- Cheon, S.-H., Lee, Y.-N., Kang, S.-I., Kye, S.-J., Lee, E.-K., Heo, G.-B., Lee, M.-H., Kim, J.-W., Lee, K.-N., Son, H.-M. & Lee, Y.-J. 2018. Genetic evidence for the intercontinental movement of avian influenza viruses possessing North American-origin nonstructural gene allele B into South Korea. *Infection, Genetics and Evolution* 66: 18–25.
- Deng, X., Zhao, Q., Fang, L., Xu, Z., Wang, X., He, H., Cao, L. & Fox, A.D. 2019. Spring migration duration exceeds that of autumn migration in Far East Asian Greater White-fronted Geese (*Anser albifrons*). *Avian Research* 10: 19.
- Efron, B. 1978. Regression and ANOVA with zero-one data: measures of residual variation. *Journal of the American Statistical Association* 73: 113–121.

- Ely, C.R., Fox, A.D., Alisauskas, R.T., Andreev, A., Bromley, R.G., Degtyarev, A.G., Ebbinge, B., Gurtovaya, E.N., Kerbes, R., Kondratyev, A.V., Kostin, I., Krechmar, A.V., Litvin, K.E., Miyabayashi, Y., Mooij, J.H., Oates, R.M., Orthmeyer, D.L., Sabano, Y., Simpson, S.G., Solovieva, D.V., Spindler, M.A., Syroechkovsky, Y.V., Takekawa, J.Y. & Walsh, A. 2005. Circumpolar variation in morphological characteristics of Greater White-fronted Geese *Anser albifrons*. *Bird Study* 52: 104–119.
- Ely, C.R., Wilson, R.E. & Talbot, S.L. 2017. Genetic structure among greater white-fronted goose populations of the Pacific Flyway. *Ecology and Evolution* 7: 2956–2968.
- Ely, C.R., Dzubin, A.X., Carboneras, C., Kirwan, G.M. & Garcia, E.F.J. 2020. Greater White-fronted Goose (*Anser albifrons*), version 1.0. In S.M. Billerman (ed.), *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, New York, USA.
- Fox, A.D. & Leafloor, J.O. 2018. *A Global Audit of the Status and Trends of Arctic and Northern Hemisphere Goose Populations*. Conservation of Arctic Flora and Fauna International Secretariat, Akureyri, Iceland.
- Fox, A.D., Elmberg, J., Tombre, I.M. & Hessel, R. 2017. Agriculture and herbivorous waterfowl: a review of the scientific basis for improved management. *Biological Reviews* 92: 854–877.
- Fujioka, M., Lee, S.D. & Kurechi, M. 2011. Bird use of rice fields in Korea and Japan. *Waterbirds* 33: 8–29.
- Gen, H., Zhang, P., Li, Y., Hou, J., Wu, S. & Dai, J. 2017. Characteristics of soil Cu and Zn forms in wetlands with different restoration ages around the Caizi Lake, Anhui Province. *Chinese Journal of Soil Science* 48: 1256–1263.
- Hodges, J.I. & Eldridge, W.D. 2001. Aerial surveys of eiders and other waterbirds on the eastern Arctic coast of Russia. *Wildfowl* 53: 127–142.
- Jia, Q., Koyama, K., Choi, C.-Y., Kim, H.-J., Cao, L., Gao, D., Liu, G. & Fox, A.D. 2016. Population estimates and geographical distributions of swans and geese in East Asia based on counts during the non-breeding season. *Bird Conservation International* 26: 397–417.
- Kim, M.K., Lee, S. & Lee, S.D. 2016. Habitat use and its implications for the conservation of the overwintering populations of Bean Goose *Anser fabalis* and Greater White-fronted Goose *A. albifrons* in South Korea. *Ornithological Science* 15: 141–149.
- Kölzsch, A., Müskens, G.J.D.M., Kruckenberg, H., Glazov, P., Weinzierl, R., Nolet, B.A. & Wikelski, M. 2016. Towards a new understanding of migration timing: slower spring than autumn migration in geese reflects different decision rules for stopover use and departure. *Oikos* 125: 1496–1507.
- Kölzsch, A., Müskens, G.J.D.M., Szinai, P., Moonen, S., Glazov, P., Kruckenberg, H., Wikelski, M. & Nolet, B.A. 2019. Flyway connectivity and exchange primarily driven by moult migration in geese. *Movement Ecology* 7: 3.
- Krechmar, A.V. & Kondratyev, A.V. 2006. *Anseriformes Birds of North-East Asia*. NERC FEB, Russian Academy of Sciences, Magadan, Russia.
- Litvin, K.E. 2011. Greater White-fronted Goose. In E.E. Syroechkovskiy (ed.), *Field Guide to Anseriformes Birds of Russia*, pp. 64–66. Anseriformes Working Group, All-Russian Scientific Institute and Museum, Moscow, Russia.
- Ministry of the Environment of the Government of Japan. 2019. *Japan Integrated Biodiversity Information System*. Ministry of the Environment, Tokyo, Japan. Available at http://www.gankamo/gankamo_top.html (last accessed on December 12 2019). [In Japanese.]

- Mooij, J.H. & Zöckler, C. 2000. Reflections on the systematics, distribution and status of *Anser albifrons*. *Casarca* 6: 92–107.
- Moriguchi, S. 2019. Wataridori Magan no Identeki Kouzou kara Mieru Furaiwei no Hozenkanri. In K. Ueda (ed.), *Idennsbi kara Tokiakasu Tori no Fushigina Sekai*, pp. 369–385. Isshiki shuppan, Tokyo, Japan. [In Japanese.]
- Moriguchi, S., Amano, T. & Ushiyama, K. 2013. Creating a potential distribution map for Greater White-Fronted Geese wintering in Japan. *Ornithological Science* 12: 117–125.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S. & Van Willigen, B. 2020. Package 'nlme'. *Linear and Nonlinear Mixed Effects Models. Version 3.1*. Available at <https://CRAN.R-project.org/package=nlme> (last accessed 23 October 2020).
- R Core Team. 2020. *R: a Language and Environment for Statistical Computing* [3.6.3]. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.R-project.org/> (last accessed 23 October 2020).
- Ramsar Convention Secretariat. 2010. *Designating Ramsar Sites: Strategic Framework and Guidelines for the Future Development of the List of Wetlands of International Importance*. Ramsar Handbooks for the Wise Use of Wetlands, 4th Edition, Vol. 17. Ramsar Convention Secretariat, Gland, Switzerland.
- Shimada, T. & Mizota, C. 2011. Fluctuation in food resources for, and crop damage by, Greater White-fronted Geese in relation to agriculture in Japan. *Japanese Journal of Ornithology* 60: 52–62. [In Japanese with English summary.]
- Shimada, T., Hatakeyama, S., Miyabayashi, Y. & Kurechi, M. 2005. Effects of climatic conditions on the northward expansion of the wintering range of the Greater White-fronted Goose in Japan. *Ornithological Science* 4: 155–159.
- Shimada, T., Mori, A. & Tajiri, H. 2019. Regional variation in long-term population trends for the Greater White-fronted Goose *Anser albifrons* in Japan. *Wildfowl* 69: 105–117.
- Si, Y., Xu, Y., Xu, F., Li, X., Zhang, W., Wielstra, B., Wei, J., Liu, G., Luo, H., Takekawa J., Balachandran S., Zhang, T., de Boer, W.F., Prins, H.T. & Gong, P. 2018. Spring migration patterns, habitat use, and stopover site protection status for two declining waterfowl species wintering in China as revealed by satellite tracking. *Ecology and Evolution* 8: 6280–6289.
- Solovyeva, D.V., Koyama, K. & Vartanyan, S. 2019. Living child-free: proposal for density-dependent regulation in Bewick's Swans *Cygnus columbianus bewickii*. *Wildfowl* (Special Issue No. 5): 197–210.
- Takekawa, J.Y., Kurechi, M., Orthmeyer, D.L., Sabano, Y., Uemura, S., Perry, W.M. & Yee, J.L. 2000. A Pacific spring migration route and breeding range expansion for greater white-fronted geese wintering in Japan. *Global Environmental Research* 4: 14.
- Takekawa, J.Y., Newman, S.H., Xiao, X., Prosser, D.J., Spragens, K.A., Palm, E.C., Yan, B., Li, T., Lei, F., Zhao, D., Douglas, D.C., Muzaffar, S.B., Ji, W. 2010. Migration of waterfowl in the East Asian flyway and spatial relationship to HPAI H5N1 outbreaks. *Avian Diseases* 54: 466–476.
- Wetlands International. 2019. *Waterbird Population Estimates*. Wetlands International, Ede, the Netherlands. Available at wpe.wetlands.org (last accessed 17 October 2020).
- Wilson, R.E., Ely, C.R. & Talbot, S.L. 2018. Flyway structure in the circumpolar greater white-fronted goose. *Ecology and Evolution* 8: 8490–8507.
- Wood, K.A., Brown, M.J., Cromie, R.L., MacKenzie, C., Newth, J.L., Pain, D.J., Perrins, C.M. & Rees, E.C. 2019. Regulation of lead fishing weights results in mute swan population recovery. *Biological Conservation* 230: 67–74.

- Xu, W., Fan, X., Ma, J., Pimm, S.L., Kong, L., Zeng, Y., Li, X., Xiao, Y., Zheng, H., Liu, J., Wu, B., An, L., Zhang, L., Wang, X. & Ouyang, Z. 2019. Hidden loss of wetlands in China. *Current Biology* 29: 3065–3071.
- Yamaguchi, N. & Higuchi, H. 2008. Migration of birds in East Asia with reference to the spread of avian influenza. *Global Environmental Research* 41–54.
- Zhao, M., Cong, P., Barter, M., Fox, A.D. & Cao, L. 2012. The changing abundance and distribution of Greater White-fronted Geese *Anser albifrons* in the Yangtze River floodplain: impacts of recent hydrological changes. *Bird Conservation International* 22: 135–143.
- Zhao, Q., Wang, X., Cao, L. & Fox, A.D. 2018. Why Chinese wintering geese hesitate to exploit farmland. *Ibis* 160: 703–705.
- Zhou, S., Yang, S., Bao, M., Yang, Y. & Li, C. 2019. Predicting the impact of the water transfer project from Yangtze River to Huai River on habitats of wintering waterbirds in Caizi Lake using remote sensed images. *Ecological Science* 38: 71–78.
- Zou, Y.-A., Tang, Y., Xie, Y.-H., Zhao, Q.-H. & Zhang, H. 2017. Response of herbivorous geese to wintering habitat changes: conservation insights from long-term population monitoring in the East Dongting Lake, China. *Regional Environmental Change* 879–888.



Photograph: Greater White-fronted Geese drinking, by Graham Maples/WWT.