Population trends and migration routes of the East Asian Bean Goose *Anser fabalis middendorffii* and *A. f. serrirostris*

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Abstract

Our ability to define the population status, migration routes and seasonal distribution of Bean Geese *Anser fabalis* throughout the annual cycle in East Asia is severely compromised by the presence of two subspecies (Eastern Taiga Bean Goose *A. f. middendorffii* and Eastern Tundra Bean Goose *A. f. serrirostris*), which are difficult to differentiate in the field. In this analysis, using tracking data from telemetry-tagged geese, count survey data and expert knowledge, we attempt to update assessment of the ranges covered by both subspecies of Bean Goose in East Asia. We suggest that, in summer, the Eastern Tundra Bean Goose extends from the Taimyr Peninsula in the west to the Anadyr River in the east. Taiga Bean Geese breed further south in the taiga zone, and results indicate that they occur in north-western Mongolia, Yakutia and the Kamchatka Peninsula during the summer months. The winter distribution of both subspecies extends through China, Japan and South Korea. Tracking data from 154 individuals revealed a major overlap in the migration routes of Tundra Bean Geese wintering in China, South Korea and Japan, but discrete flyways for Taiga Bean Geese wintering in different regions. Long-term ground surveys carried out in the wintering range showed that numbers of Bean Geese in China and South Korea have increased significantly, to *c.* 253,100 and 88,300 individuals, respectively, of which roughly 10% are considered to be Taiga Bean Geese, about which subspecies we need to know more. Numbers of Japanese-wintering Bean Geese are increasing more slowly, with totals currently at *c.* 10,300 (*c.* 900 Tundra Bean Geese and *c.* 9,400 Taiga Bean Geese). On the basis of these national and flyway estimates, derived from counts over the last five years, we identify new key wintering sites for the species in East Asia. Distributional changes at sites in China showed that wintering Bean Geese (most likely of the Tundra form) have become more widespread and numerous in the Yangtze River floodplain since the early 2000s. We argue for future strengthening of international cooperation to continue tracking and monitoring of Bean Geese, to provide a sound scientific basis for the effective management and protection of the flyway populations of both Bean Goose subspecies throughout East Asia.

Key words: Bean Goose, China, distribution range, East Asia, Japan, Korea, migration flyway, population trends.

The Bean Goose *Anser fabalis* (hereafter BG) is classified by IUCN as of "least-concern", on considering its abundance at the global level (BirdLife International and Handbook of the Birds of the World 2019). The species has two forms, one breeding mainly in tundra habitats (the two subspecies Western Tundra BG *A. f. rossicus* and Eastern Tundra BG *A. f. serrirostris*, although the status of these subspecies is currently under discussion; Solovyeva *et al.*, pers. comm.). The other breeds in taiga forests (subspecies Western Taiga BG *A. f. fabalis* and Eastern Taiga BG *A. f. middendorffii*; Fox & Leafloor 2018). Ottenburghs *et al.* (2020) have shown that Western Tundra and Taiga BG are genetically distinct, and can therefore be treated as subspecies. However, the distinction between taiga and tundra forms of BG complicates their global conservation, as they are similar in appearance and overlap to varying degrees on the wintering grounds (*e.g.* Mooij & Zöckler 1999; Marjakangas *et al.* 2015). The population structure and facets of its ecology in Europe are reasonably well known (Sutherland & Allport 1994; VanImpe 1996; Mitchell *et al.* 2016; Fox *et al.* 2017; Honka *et al.* 2017) but, even here, a lack of basic knowledge on its migration routes greatly hinders effective management of the constituent flyway populations (Marjakangas *et al.* 2015; Johnson *et al.* 2018).

Further east, Heinicke (2009) reviewed the status and possible flyway population structure of the BG in central Asia. More recently, Rozenfeld *et al.* (2018) showed that at least some Taiga BG in central Asia belong to the Western Taiga BG subspecies, with breeding grounds in eastern parts of the Yamalo-Nenets Autonomous District and wintering grounds in Xinjiang Province, western China. This population will not be considered further in the present analysis (*i.e.* Western Taiga BG counts from Xinjiang are not included), because we focus here on the Eastern Tundra and Taiga BG populations.

The Eastern Tundra BG and Eastern Taiga BG both occur in Japan, Korea and eastern parts of China during winter, but knowledge about their relative distribution, abundance and habitat use is hindered by the difficulty of differentiating the two subspecies in the field. Before 2012, BG appear to be the only goose species in China which has increased significantly, at least in the Yangtze River floodplain (Jia *et al.* 2016), possibly because BG represent an exception to the rule for wild geese in the region by frequently feeding on farmland (Park & Won 1993; Fox 2005; Si *et al.* 2018). However, definite separation between subspecies could not be made in the study of Jia *et al.* (2016). To be able to separate and assess differing population trends and conservation needs for the Eastern Tundra and Taiga BG, it is important first to establish their relative distributions, for instance by using telemetry data to establish the migratory connectivity between their summering and wintering grounds. This improved knowledge of their distributions can then inform assessment of the abundance and trends in numbers for BG subspecies in East Asia.

Despite some observational data (*e.g.* Ikawa & Ikawa 2013) and limited telemetry and neck-collar resighting studies (Guo *et al.* 2015; Si *et al.* 2018; Li *et al.* 2020), we previously lacked tracking data from individual BG to establish relationships between breeding, moulting, staging and wintering areas to underpin the definition of biogeographical populations in East Asia. Fox & Leafloor (2018) identified six such populations of the two subspecies as follows: 1) *A. f. middendorffii*, Okhotsk/ Kamchatka–Japan; 2) *A. f. middendorffii*, Yakutia–East China; 3) *A. f. middendorffii*, Sayan–East China; 4) *A. f. serrirostris*, Russia–Japan; 5) *A. f. serrirostris*, Russia–Korea; and 6) *A. f. serrirostris*, Russia–China. However, again, in the absence of telemetry data, those authors were unable to confirm the relationships between wintering and summering ranges and therefore migratory connectivity of these populations. This lack of knowledge hinders assessment of population trends and status, which is required if conservation programmes developed for the protection and management of this species are to be effective.

Here we aim to update knowledge on the summer and winter distribution of BG in East Asia, using recently published data, new information from telemetry studies and expert opinion to identify the geographical ranges of the different flyway populations throughout their annual cycle. We also attempt to clarify, as far as possible, the status and abundance of population in their wintering ranges.

Methods

Migration data

To delineate the migratory flyways of the different populations of BG in East Asia, a total of 264 BG were caught and tagged with Global Positioning System (GPS) transmitters in East Asia during 2015–2018, including 191 birds at five key sites in summer, and 73 birds in two key wintering areas (Table 1). Of these, 154 individuals with at least one complete spring or autumn migration episode were used to contribute data to identify the flyway corridors (Table 2). A total of 171 BG (73 adults: 25 males, 23 females and 25 with unknown sex; 97 juveniles: 29 males, 16 females and 52 with unknown sex; and a single bird of unknown age and sex) were captured on the

Table 1. Summary table of 264 Bean Geese caught and fitted with solar-powered GPS/GSM telemetry devices in East Asia during 2015–2018, including 191 birds at eight sites across the summering range, and 73 birds at three key wintering sites, showing age, sex and numbers caught at each site.

	Capture sites	Coordinates		Capture period	Age			Sex			Total no. of geese
		Latitude	Longitude		Adult	Juvenile	Unknown	Female	Male	Unknown	
Summering area	Lena Delta, Russia	72.47	126.37	2017	36	0	0	19	17	0	36
(*n* = 191)	Indigirka River, Russia	70.60	151.72	2018	15	0	0	0	0	15	15
	Chaun Delta, Russia	69.00	169.18	2016	0	14	0	5	5	4	14
	Chaun Delta, Russia	68.88	170.96	2017	12	58	0	14	32	24	70
	Chaun Delta, Russia	68.82	167.62	2018	7	23	0	1	0	29	30
	Amyl River, Russia	53.29	93.57	2017	2	2	0	2	2	0	4
	Amyl River, Russia	53.28	93.57	2018	1	0	1	1	0	1	2
	Tunamal Lake, Mongolia	49.42	98.48	2017	20	0	0	8	12	0	20
Wintering area	Anhui Lakes, Yangtze R., China	30.90	117.67	2015–2017	42	0	6	25	22	1	48
(*n* = 73)	Poyang Lake, Yangtze R., China	29.12	116.27	2015–2016	11	0	4	6	9	0	15
	Jianghua Bay, South Korea	37.28	126.77	2017	0	0	10	0	0	10	10

Table 2. Summary of satellite tracking data recorded from 154 successful tracked Bean Geese during 2015–2019, which provided the basis for determining the two subspecies in East Asia. A total of 91 spring and 211 autumn tracks include 79 spring and 186 autumn tracks of 134 birds from the East Asian flyway of the Tundra Bean Goose, which were caught at their main summering area (Lena Delta, Chaun Delta and Indigirka River) and wintering sites (the Yangtze River floodplain and Jianghua Bay); and 12 spring and 25 autumn tracks of 20 Taiga Bean geese from the East Asian Continental flyway, caught at their main summering area (Amyl River and Tunamal Lake) and wintering site (the Yangtze River floodplain). The tracks of Eastern Taiga Bean Geese on the West Pacific flyway are from Shimada (2019). Note: ? = numbers of tagged geese not known.

Subspecies	Flyways	Capture sites	Tracking period	No. of geese	Spring	Autumn	Migration routes
Eastern Tundra BG	East Asian flyway	Lena Delta, Russia	2017	33	24	56	Lena Delta–E China
		Indigirka River, Russia	2018	13	0	13	Indigirka River–E China/South Korea
		Chaun Delta, Russia	2016–2018	62	22	84	Chaun Delta–E China/South Korea/Japan
		Yangtze River, China	2015–2017	22	29	30	Russian tundra–E China
		Jianghua Bay, South Korea	2017	4	4	3	Russian tundra–South Korea
		Total	**2015–2018**	**134**	**79**	**186**	
Eastern Taiga BG	East Asian Continental flyway	Amyl River, Russia	2017–2018	6	2	7	Sayan–Yangtze River
		Tunamal Lake, western Mongolia	2017	13	9	18	western Mongolia–Yangtze River
		Yangtze River, China	2016	1	1	0	Yakutia–Yangtze River
		Total	**2016–2018**	**20**	**12**	**25**	
	West Pacific flyway	?	?	?	?	?	Kamchatka–Japan
		Overall total		**154**	**91**	**211**	

summering areas in arctic Russia. These were distributed between the Chaun River delta (68°53'N, 170°58'E, n = 114), the Lena Delta (72°28'N, 126°22'E, n = 36), the Indigirka River (70°45'N, 151°28'E, n = 15) and the Amyl River (53°17'N 93°34'E, n = 6) between July and August, from 2016 to 2018. Twenty BG (all adults: 12 males and eight females) were captured at Tunamal Lake in the Mongolian summering range (49°25'N, 98°29'E) in July 2017. Another 73 BG (53 adults: 27 males, 25 females and one of unknown sex; four males of unknown age, six females of unknown age, and ten birds of unknown age and sex) were captured on their wintering grounds (Yangtze River floodplain, China 30°54'N, 117°39'E, n = 63 and Jianghua Bay, South Korea 37°17'N, 126°46'E, n = 10) during November–March in 2013–2017 (Table 1, Supporting Materials Table S1). Geese were caught on the wintering grounds in the beams of powerful lamps and captured in hand nets using boats at night, or in heavy-duty mist-nets (designed for catching large birds) set at their roosts. In summer, flightless birds were rounded up and caught on their moulting areas, by driving them with boats from the safety of water into movable funnel nets and pens established on the shore. Several geese were caught with the help of a trained dog.

Captured geese were fitted with different collar- or backpack-mounted solar-powered transmitters (Druidtech, China, 35 g or 45 g, mounted on neck bands; Ecotone, Poland, 25–72 g, mounted on neck bands or by using backpacks; KoEco, South Korea, 72 g, using back packs; or Ornitela, Lithuania, 35 g or 45 g, mounted on neck bands). All recorded time-stamped GPS positions, transmitted via the Global System for Mobile Communications (GSM) mobile networks to download for analysis. The total weight of any of the transmitters on the bird was < 3% of its body mass (Sokolov 2011). The transmitters provided 120 ± 72 (mean ± s.d., range = 4–261) GPS positions per day, depending upon power supply (Supporting Materials Table S1). We only used data from individuals with at least one complete spring or autumn migration to contribute to the identification of flyway structure. Movement data from the first day after birds were captured and the last day before birds died or contact was lost from the loggers were excluded from all analyses, in case bird behaviour on these occasions was aberrant or atypical.

Distribution and migration range

The core BG distribution range was defined in ArcGIS 10.2 (ESRI 2013) from the maps of BirdLife International and Handbook of the Birds of the World (2019). We updated these maps based on information forthcoming on distribution ranges data compiled from a number of sources. These included wintering counts (see *Abundance and trends of wintering population* below) and data on summer, migration and winter distributions of tagged individuals (see *Migration data* above). These sources of information were combined with that from Fox & Leafloor (2018), Honka *et al.* (2017), Ruokonen *et al.* (2008), Cao *et al.* (2010), Gerasimov *et al.* (2010), Krechmar & Kondratiev (2006), and Goroshko (2012), and with expert knowledge of areas used by the geese across their range. As far as possible, we attempted to define East Asian BG migration flyways based on tracking data and the literature review (Emelyanov 2000; Shimada 2019). All data sources were discussed, and the distribution and migration routes agreed by 18 BG flyway experts from six countries on the East Asia flyway, during a symposium held in Beijing during October 2019 (Supporting Materials Table S2).

Population estimates and trends in abundance in three management units

BG in East Asia were previously aggregated into three management units, based on wintering provenance, namely China, South Korea and Japan (Fox & Leafloor 2018).

The changes in annual wintering abundance in China prior to 2011/12 were derived from Jia *et al.* (2016) supplemented in 2003/04, 2004/05, 2015/16, 2017/18, 2018/19 and 2019/20 by counts recorded during synchronous Yangtze waterbird surveys undertaken from mid-December to early February. These surveys are considered to have covered the vast majority of wintering BG in China (Cao *et al.* 2010; Jia *et al.* 2016). The survey methods used in 2015/16 and 2017/18–2019/20 were consistent with those 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). However, coverage was slightly extended because some new survey sites were added, as a result of information gained from the satellite tracking data for BG in 2018/2019 and 2019/2020. While we know that there were wintering BG elsewhere in China, away from the Yangtze River floodplain, coverage of these sites has been incomplete, but they are considered to contribute relatively small numbers (Cao *et al.* 2010; Jia *et al.* 2016). For this reason, we present trends in wintering abundance for all BG and for the two subspecies populations in the time series from the Yangtze River floodplain only. However, when attempting to estimate the recent wintering numbers to compare and add to those from Korea and Japan, we supplemented the Yangtze River floodplain data with counts from surveys conducted in the Huai River, the Yellow River floodplain and the coastal areas of East China in winters 2006/07–2018/19 (see below), which are also supported by the winter distributions of tagged individuals (Supporting Materials Table S3).

Since 1999, the Korean Ministry of Environment and its associated institutes – the National Institute of Environmental Research (until 2007) and the National Institute of Biological Resources (since 2008) – have coordinated annual nationwide censuses at most lakes, reservoirs, lengths of seashore and bays in South Korea known to be important for waterbirds. The simultaneous two-day field counts, made in mid- or late January each year, are undertaken by ornithologists, experienced birdwatchers and volunteers to estimate the distribution and abundance of wintering waterbirds in South Korea.

In Japan, the Ministry of the Environment has conducted the "*Annual Census on Waterfowl (Anatidae) Populations*" with the assistance of prefectural governments, in mid-winter (*c.* 15 January) each year since

1970. 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).

Simple linear regressions were taken as the default approach to the analysis of $\log_{10}(x + 1)$-transformed annual count data to detect the general trends for the three population units: Japan, China and South Korea. Temporal trends in counts of long-lived waterbirds may be temporally autocorrelated (*e.g.* Wood *et al.* 2019), so initial assessments were made of linear regression residuals for the temporal trends in count data for each country, fitted using the nlme package in Program R (Pinheiro *et al.* 2020; R Core Team 2020). Inspections of the resulting autocorrelation plots showed evidence of statistically significant ($P < 0.05$) residual temporal autocorrelation in the regression models for both China and Japan, but not South Korea. 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 = 2, South Korea = 0, and Japan = 1. 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:

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

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).

In using the recent count data to estimate current population size, we have adopted different techniques for the different countries. The abundance estimates of BG in China were based on total counts of wintering surveys, including the average counts from the Yangtze River floodplain during 2017/18–2019/20 and the maximum counts from 2015/16–2018/19 in the Huai River, the Yellow River floodplain, and the coastal areas of East China. In other countries, population estimates of BG were based on average counts of the most recent available five years of counts from South Korea (2015/16–2019/20) and Japan (2014/15–2018/19).

Note that throughout, because of the lack of identification to subspecies of BG associated with many historical count data, we are unable with confidence to present separate estimates for *A. f. middendorffii* and *A. f. serrirostris*. However, we have tried to assign counts to the two subspecies following the methods of Jia *et al.* (2016), who assigned counts to *A. f. middendorffii* and *A. f. serrirostris*, based on current knowledge and expert local opinion. To generate population estimates for the races of BG, we made the highly conservative, but reasonable worst-case assumption that in China *A. f. middendorffii* occur almost exclusively at Dongting Lake while *A. f. serrirostris* is distributed more widely elsewhere. *A. f. serrirostris* is the dominant and widespread subspecies in South Korea, while *A. f. middendorffii* is restricted to a few wetlands in the Nakdong River watershed, such as the Upo Wetland and Junam Reservoir (Park 2002). Besides that, most BG occurring in Japan are *A. f. middendorffii*, where the main wintering area used by the less common *A. f. serrirostris* is thought to be limited to two marshes in Miyagi Prefecture during the northern winter.

Key wintering sites in East Asia

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

Changes in the number and distribution of the species at key sites in China over the past 15 years were investigated by comparing annual maximum counts at these sites from 2003/04 to 2019/20, taking into account the general improvement in coverage over this period. In addition to the survey data mentioned in *Population estimates and trends in abundance* above, surveys of key sites (Poyang Lake, Dongting Lake, Hubei, and Anhui Lakes) along the Yangtze River floodplain in winters 2002/03, 2007/08 to 2014/15, and 2016/17 were also included (Table 5).

Results

Summering and wintering distribution range

East Asian BG show a wide summering range, in the taiga zone from northwest Mongolia to Far East Russia, and in the tundra zone from the Taimyr Peninsula to the Anadyr River (Fig. 1). This study attempted as far as possible to distinguish between the subspecies when differentiating the summering areas of BG in East Asia (Ruokonen *et al.* 2008; Honka *et al.* 2017; Fox & Leafloor 2018). This is possible because both subspecies were tracked from their breeding grounds, where subspecies can be separated, as well as from the wintering grounds.

The telemetry data suggest that the summering range of Eastern Tundra BG stretches from the Pyasina River in the western part of the Taymyr Peninsula (73°46'N, 87°16'E) in the west, to the mouth of the Anadyr River, Chukotka (64°50'N, 178°56'W), in the east (Fig. 1). This confirms that the subspecies is confined to the tundra zone in summer (62°–73°N) in an almost continuous distribution, except for a conspicuous gap along the arctic coast between the Chaun Delta and the Anadyr River estuary (Fig. 1). Unfortunately, although we have many tagged Eastern Tundra BG summering in the far west of the breeding range, we still have too little information on the current extent of the Western Tundra BG *A. f. rossicus* to be able to delineate the interface and degree of overlap (if any) of these two forms.

In contrast, we caught only modest numbers of Eastern Taiga BG, several of which were captured at their summer quarters, so we are not in a position to conclude much about the breeding ranges of these populations relative to their respective wintering areas. Nevertheless, the observed

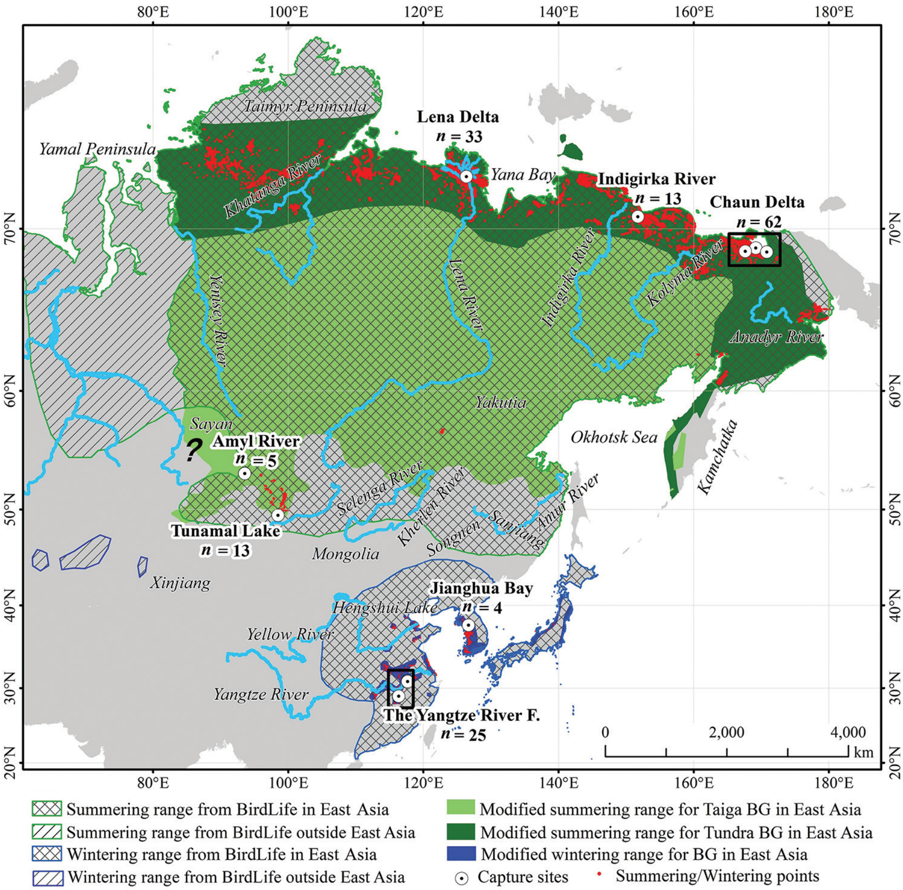

Figure 1. Revised distribution map of the Eastern Taiga Bean Geese *Anser fabalis middendorffii* and Eastern Tundra Bean Geese *A. f. serrirostris* in East Asia, modified from BirdLife International and Handbook of the Birds of the World (2018) (shown by a black grid). Summering (light green = Eastern Taiga Bean Geese; dark green = Eastern Tundra Bean Geese) and wintering (blue = Eastern Bean Geese) ranges are illustrated. Revision of the summer distribution is based on tracking data (red dots = GPS positions between the dates of last arrival and first departure in summer), expert knowledge and a review of the literature (including Fox & Leafloor 2018; Honka *et al.* 2017; Ruokonen *et al.* 2008; Cao *et al.* 2010; Gerasimov *et al.* 2010; Krechmar & Kondratiev 2006; and Goroshko 2012). The revised wintering range was based on field surveys data, tracking data and expert knowledge (see *Methods* for details). Two hundred and sixty-three individuals were caught in five key areas (Tunamal Lake in Mongolia; and the Amyl River, Lena River delta, Indigirka River and Chaun River delta in Russia) across the summer range and at two key wintering areas (the Yangtze River floodplain, China, and Jianghua Bay, South Korea) to validate and supplement expert knowledge of the species in East Asia. Circles with black dots = capture sites, *n* = number of birds that completed at least one spring or autumn migration, in total 154 individuals (Table 2). All the site/area names mentioned in the paper are illustrated on the map.

summer movements of tagged birds confirmed the breeding populations as previously outlined, with isolated Altay-Sayan/Mongolia and Kamchatka breeding populations, and we suspect that the subspecies has a large summering range, extending across the taiga biome of Krasnoyarsk (including the Putorana Plateau) and through the Yakutia, Magadan and Khabarovsk regions of Russia (Emelyanov 2000; Gerasimov *et al.* 2010; Fox & Leafloor 2018).

Regarding new changes made to the former distribution map, we have removed the northern section of the Taimyr Peninsula indicated by BirdLife International and Handbook of the Birds of the World (2019). Gerasimov *et al.* (1989) recommended expanding the distribution of two subspecies of Eastern BG to the Kamchatka Peninsula, and Emelyanov (2000) recommended reducing the summering range of Eastern Taiga BG in China and southern Russia. Since 2011, there has been a gradual expansion in the area occupied by Taiga BG in summer in Zabaikalsky Krai in Russia, although it is considered that is merely recent recolonisation of formerly occupied areas (O. Goroshko, unpubl. data). Based on satellite tracking data, we have also expanded the distribution of BG in northern Kazakhstan, Sayan and Altai Zone in Russia, but further north, we still have little idea about the interface between the breeding area of *A. f. middendorffii* and *A. f. fabalis*. While we consider it highly unlikely that the breeding range of either Taiga BG extends all the way north to the southern boundary of breeding *A. f. serrirostris*, until more information is forthcoming, we can offer no more accurate information about the true summer distribution of Eastern Taiga BG.

Combining the satellite tracking data, wintering survey data, and literature analyses, the wintering distribution areas of the three BG management units have all been reduced in extent to reflect our improved knowledge in recent years (rather than reflecting any major range contraction). The distribution in China is concentrated in the wetlands in the floodplain of the Yangtze River, the Yellow Sea wetlands in Yancheng, Jiangsu, the Yellow River estuary, and Hengshui Lake in Hebei. BG in South Korea mainly winter on the Yellow Sea coast in the west and the East China Sea coast in the south, and in Japan they winter mainly on the eastern coast in the Sea of Japan and the Pacific coast.

East Asian migration routes

Based on the results from telemetry, the two subspecies in East Asia are sympatric on the wintering grounds, but the summering range of the Tundra BG lies well to the north of that of the Taiga BG, so migration distances are therefore greater. The telemetry data suggests potentially three BG flyways overall (Fig. 2, Fig. 3), although we need more tracking results to provide a better definition of these routes.

The East Asian flyway of Eastern Tundra BG was determined from tracks of 134 individuals with complete migration data, including 186 autumn tracks and 79 spring tracks (Fig. 2). Of 107 birds captured in the Lena River delta, the Indigirka River and the Chaun River delta, all migrated along the rivers within the taiga forest and flew down

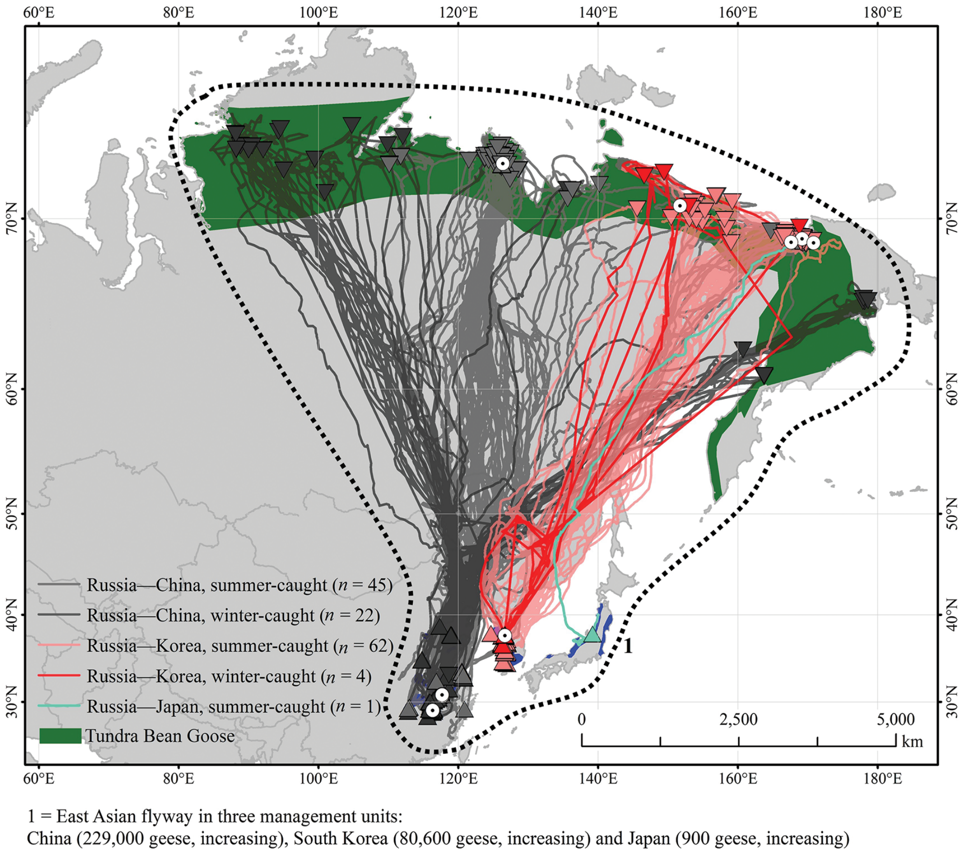

Figure 2. The East Asian flyways of Eastern Tundra Bean Geese described in East Asia (black dashed line: tracked birds caught in summer, between the Lena River delta and the Chaun River delta in Russia, wintered in China, South Korea and Japan; and tracked birds caught whilst wintering in China which summered between the Taimyr Peninsula in the west and the Anadyr River in the east). These definitions are based on migration routes recorded for the Russia–China flyway population (black solid lines = birds caught in winter, *n* = 22; grey solid lines = birds caught in summer, *n* = 45), the Russia–Korea flyway population (red solid lines = birds caught in winter, *n* = 4; light red solid lines = birds caught in summer, *n* = 62), and the Russia–Japan flyway population (tourquoise solid lines = birds caught in summer, *n* = 1), respectively. Information from 134 individuals caught in five key areas across the range (circles with black dots = capture sites) were combined with expert knowledge (see text for details) in order to improve delineation of the summer distribution. Green shaded areas = our suggestion for revising the summering range; dark blue areas = revised wintering range. Inverted and regular triangles = summering and wintering areas used by tracked individual(s), respectively. Population sizes and trends are from the results from this study, based on count data from China (1998/99–2019/20), Korea (1998/99–2019/20), and Japan (1969/70–2018/19).

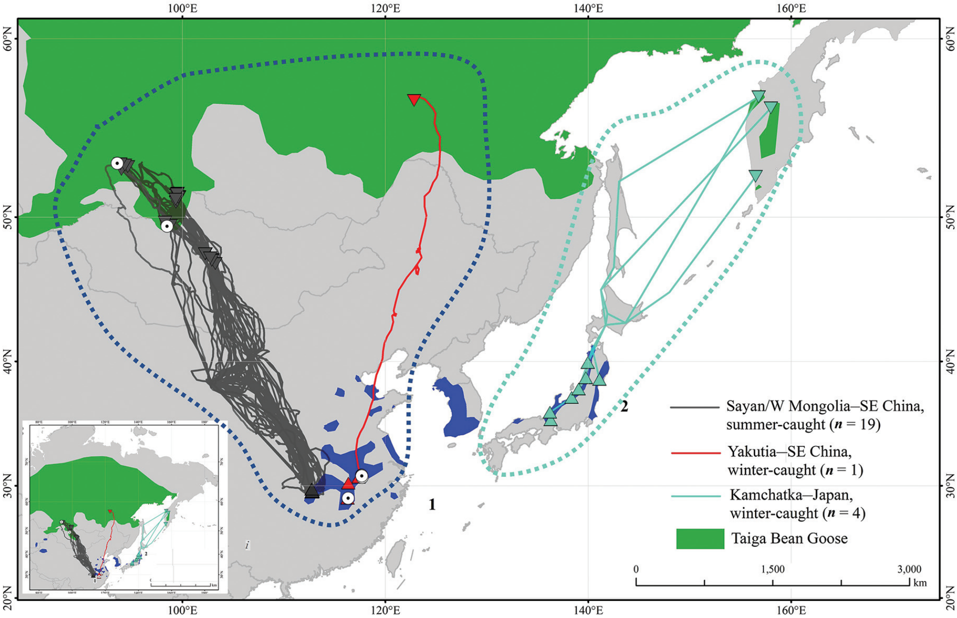

Figure 3. Two distinctive flyways described for Eastern Taiga Bean Geese in East Asia: (1) the East Asian Continental flyway (dark blue dashed line: birds which summered on the Amyl River in Russia and Tunamal Lake in Mongolia, wintered in China; and birds which wintered in China, summered in Yakutia in Russia), and (2) the West Pacific flyway (turquoise green dashed line: birds wintered in Japan, summered in Kamchatka). These definitions are based on migration routes of the Sayan–SE China flyway population (black solid lines = birds caught in the summering range, n = 19), the Sayan/W Mongolia–SE China flyway population (red solid line = bird caught in the wintering range, n = 1), and the Kamchatka–Japan flyway population (turquoise green solid lines = birds caught in the wintering range, n = 4), respectively. Information from 20 individuals caught in 4 key areas across the range (circles with black dots = capture sites) were combined with expert knowledge (*see text for details*) and Shimada (2019). The green shaded areas indicate our revised suggestion for the summering range and the dark blue areas represent that for the revised wintering range. Inverted and regular triangles represent summering and wintering areas used by tracked individual(s), respectively. Population sizes and trends are from the results from this study, based on count data from winter surveys in China (1998/99–2019/20), Korea (1998/99–2017/18), and Japan (1969/70–2018/19).

through the Songnen and Sanjiang plains of northeast China. Here, geese either proceeded further to the south and wintered in East China (including the Yangtze River floodplain, Yellow Sea wetlands in Yancheng, Yellow River estuary and Hengshui Lake), or moved to the east to winter in South Korea and Japan. The 26 birds captured in China and South Korea all summered in the arctic tundra, specifically south of the Taimyr Peninsula, the Lena Delta, around Yana Bay and in the lower Anadyr River. These birds followed similar migration routes to those birds tracked from the breeding grounds.

Some tracked geese changed wintering areas within and between years. Of 44 individuals with multiple years of tracking data, nine individuals (20%) switched between wintering sites in China and Korea from one year to the next, of which five individuals visited both countries within one winter season. Geese from wintering locations in Eastern China bred up to the mouth of the Anadyr River in the east, thereby showing overlap with the range of geese wintering in Korea, which have a more eastern breeding distribution up to Svyatoy Nos Cape (72°43'N, 140°58'E) in the west (Fig. 2). Eastern Tundra BG breeding on the Kamchatka Peninsula are known to migrate to China and Korea to winter (Gerasimov *et al.* 2010).

Based on our extremely limited telemetry data derived from Eastern Taiga BG in the East Asian Continental flyway, these birds can likely be divided into two migration routes which differ in summering areas. The first involves geese from the Sayan/W Mongolia–SE China flyway, defined by 19 individuals with full migration data, including 25 autumn tracks and 11 spring tracks (Fig. 3). Eastern Taiga BG in this flyway were captured on summering grounds in western Mongolia, Sayan and Altai in Russia and wintered mainly at Dongting Lake (Jia *et al.* 2016). A single bird (bg010) summered in Yakutia, Russia, migrated through northeast China, and wintered in Poyang and Anhui Lakes in the middle and lower Yangtze River floodplain in China (Jia *et al.* 2016), showing perhaps a separate flyway (hereafter described as the Taiga BG Yakutia–SE China flyway shown in Fig. 3). Finally, the West Pacific flyway of Taiga BG was defined by observations in Japan of 731 neck-banded individuals caught in western parts of Kamchatka and two satellite tracks of Taiga BG from Japan (Fig. 3), summering in Kamchatka. Eastern Taiga BG in this flyway summered on the Kamchatka Peninsula, migrated through Sakhalin or Kuril Islands, and wintered in Japan (Gerasimov *et al.* 2010; Shimada 2019).

Population size and trends of wintering populations

The long-term count data indicated that trends in abundance of the Tundra BG and Taiga BG differed in the three wintering countries of East Asia (Fig. 4, Table 3; Supporting Materials Table S3).

The numbers of wintering BG (*i.e.* of both subspecies combined) on the Yangtze River floodplain in China have increased significantly during the review period (Table 4). Before 2010, it was estimated that there were about 100,000 BG wintering there, with numbers increasing sharply after 2015/16, to number 273,500 in 2019/20, *i.e.* an increase of 2.6 times the numbers in 2009/10 (Fig. 4, Supporting Materials Table S3).

Numbers of BG wintering in South Korea have also shown an overall increase during the 21st century (Fig. 4). From 1998/99–2003/04, the annual totals were stable at 27,700–44,100 birds, but in 2004/05 they rose markedly to 86,116, and reached 87,771 by 2019/20 (Fig. 4, Supporting Materials Table S3).

The numbers of BG wintering in Japan have steadily grown since the 1970s (Table 4).

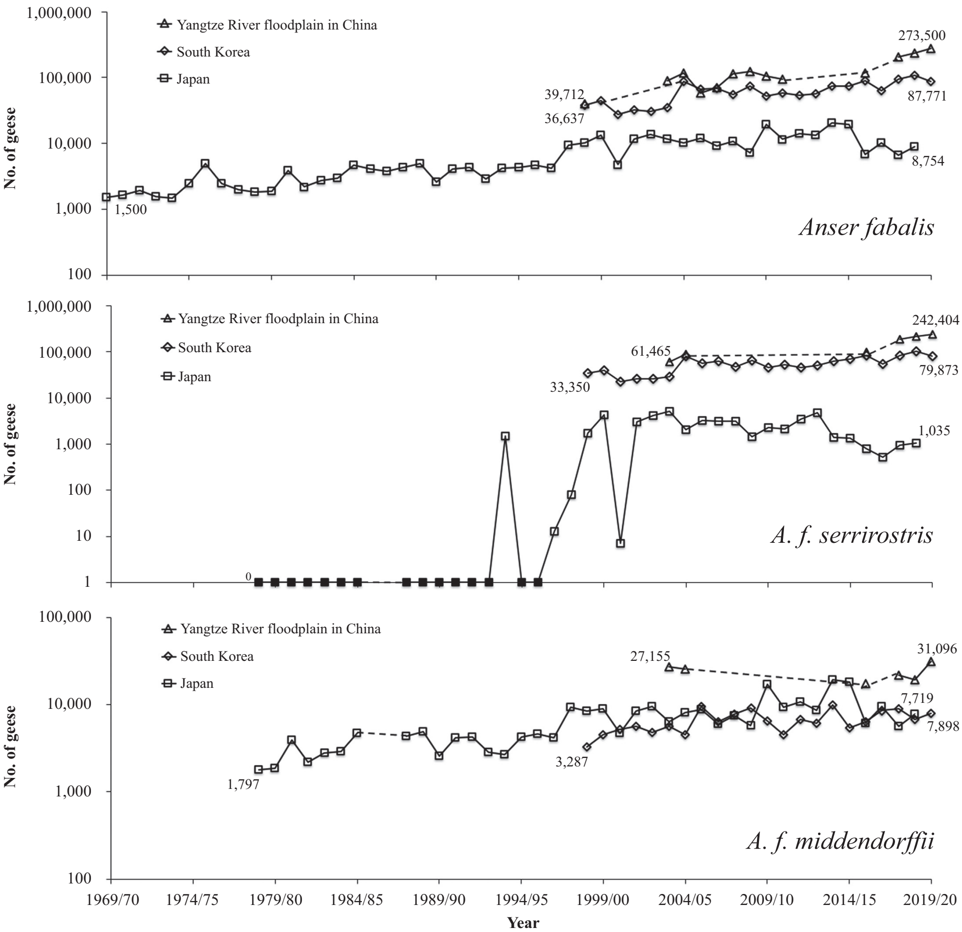

Figure 4. Abundance estimates and trends in wintering counts of all the Eastern BG combined, including *serrirostris* and *middendorffii*, top, *A. f. serrirostris* only (middle) and *A. f. middendorffii* (lower), in the three management units (China, South Korea and Japan) during 1969/70–2019/20. Japanese and South Korean population estimates derive from 1969/70–2019/20 from wintering surveys. Chinese Bean Geese population estimates during 1998/99–2010/11 were obtained from Jia *et al.* (2016), and 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 S3 for more details). Dashed lines connect counts with interim missing count data in the corresponding years. The black solid symbols indicate zero counts in those years.

Before 2000, counts of numbers of Japanese-wintering BG showed an increasing trend, peaking in 1999/2000 (at 13,148 birds), after which, counts have fluctuated considerably between 4,719 and 20,491 (Fig. 4, Supporting Materials Table S3).

From the assignment of BG to subspecies, on the basis of their different distributions

Table 3. Abundance estimates and 1% criteria for the Bean Goose flyways and for the entire Eastern population of Bean Geese, based on wintering survey data (2004/05–2019/20) in China, South Korea and Japan. The method used to calculate new population estimates for the subspecies follows Jia *et al.* (2016).

Data sources	Eastern Tundra Bean Goose			Eastern Taiga Bean Goose			Total Eastern population
	East Asian flyway			East Asian Continental flyway		West Pacific flyway	
	China	S. Korea	Japan	China	S. Korea	Japan	
Population estimates in Cao *et al.* (2008)	–	–	–	–	–	–	190,000
Population estimates in Jia *et al.* (2016)	95,000	55,000–66,000	2,500	6,000	5,000–10,000	9,500	157,000–194,000
Population estimates in Fox & Leafloor (2018)	52,000–113,000	60,000	2,000	6,000	6,000	6,000	132,000–193,000
New population estimates in 2020	229,000[a]	80,600[b]	900[c]	24,100[a]	7,700[b]	9,400[c]	351,700
New 1% criterion in 2020[d]	2,290	806	9	241	77	94	3,517

Notes: [a]new population estimate for China based on counts in winters 2006/07–2019/20; [b]new population estimate for South Korea based on mean numbers counted for winters 2015/16–2018/19; [c]new population estimate for Japan based on mean numbers counted for winters 2014/15–2018/19; [d]based on new population estimates for the Chinese, South Korean and Japanese wintering populations in 2020.

Table 4. Summary of the results from the regression models of the linear trends in Bean Goose counts for each country and each subspecies. ACS = autocorrelation structure (no. of years) included in the model.

Country	**Subspecies**	**ACS**	**Parameter**	**Estimate**	**s.e.**	***t* value**	***P* value**	**Efron's R^2**
China	*Anser fabalis*	2	Intercept	–57.433	7.136	–8.048	< 0.001	–
			Year	0.031	0.004	8.754	< 0.001	0.785
	A. f. serrirostris	0	Intercept	–55.066	14.699	–3.746	0.020	–
			Year	0.030	0.007	4.095	0.015	0.807
	A. f. middendorffii	0	Intercept	12.555	12.713	0.988	0.379	–
			Year	–0.004	0.006	–0.644	0.555	0.094
South Korea	*Anser fabalis*	0	Intercept	–36.578	7.284	–5.022	< 0.001	–
			Year	0.021	0.004	5.676	< 0.001	0.617
	A. f. serrirostris	0	Intercept	–39.233	8.145	–4.817	< 0.001	–
			Year	0.022	0.004	5.395	< 0.001	0.593
	A. f. middendorffii	0	Intercept	–19.351	6.976	–2.774	0.012	–
			Year	0.012	0.003	3.319	0.003	0.355
Japan	*Anser fabalis*	1	Intercept	–35.976	3.792	–9.487	< 0.001	–
			Year	0.020	0.002	10.467	< 0.001	0.766
	A. f. serrirostris	1	Intercept	–218.299	31.210	–6.995	< 0.001	–
			Year	0.110	0.016	7.055	< 0.001	0.678
	A. f. middendorffii	0	Intercept	–30.697	4.320	–7.107	< 0.001	–
			Year	0.017	0.002	7.976	< 0.001	0.632

in the three management units (see *Methods* for details), we can attempt to back cast trends in the two populations in each country. On this basis, numbers of both subspecies have increased in Japan since the late 1990s. Numbers of Tundra BG in China and South Korea have shown a slight increase, while those of Taiga BG in China and South Korea have remained stable (Table 4). In general, the number of Tundra BG increased 3.34-fold in the whole of East Asia, from 95,905 in 2003/04 to 320,484 in 2019/20, while the number of Taiga BG basically remained around at 30,000–34,000 birds.

Key wintering sites in three management units

In China, 20 key wintering sites for BG were identified, on the basis of *c.* 253,100 BG estimated nationally (Table 5). These include 18 key sites along the Yangtze River floodplain in Hunan, Hubei, Jiangxi, and Anhui Provinces, as well as one site in the Yellow River delta in Shandong Province, and one site in Hubei Province (Fig. 5, Table 5). Thirty-three key wintering sites for BG were identified based on the estimated population size of 88,328 geese in South Korea, the average of annual totals recorded over the last five years (Supporting Materials Table S3). They are widely distributed along the south and west coasts of South Korea (Fig. 5), roosting and foraging along rivers, on lakes and surrounding farmland, including the Iwon-myeon coast in Taean and Bunam Lake in Chungcheongnam-do, the Han River estuary in Gyeonggi-do, and Geumho Lake in Jeollanam-do, with most of the South Korean geese distributed between these sites (Supporting Materials Table S4). Sixteen key wintering sites for BG were identified based on the estimated population size in Japan (*c.* 10,311 geese) the average for the last five years (Supporting Materials Table S3), including Lake Hachirogata in Akita-ken, Lake Izunuma and Uchinuma and Lake Kabukurinuma in Miyagi-ken, Kamiike and Shimoike Pond in Yamagata-ken, and Lake Fukushimagata in Niigata, where most of the Japanese BG occur (Fig. 5, Supporting Materials Table S4).

In China, the Eastern Taiga BG is mainly confined to Dongting Lake in Hunan Province, with small numbers at Caizi Lake in Anhui Province, whereas the rest of the wetlands, which are important for BG, are thought mostly to support Eastern Tundra BG. In South Korea, the Tundra BG is the dominant and widespread subspecies, while the Taiga BG is restricted to a few wetlands in the Nakdong River watershed, such as the Upo Wetland, Junam Reservoir, lower reaches of Nakdong River and the Nakdong River estuary (Park 2002). Most BG occurring in Japan are Taiga BG. The main area used by the less common Tundra BG is limited to marshes in Miyagi Prefecture (Lake Byodonuma, Lake Kejonuma, Lake Kabukurinuma, Lake Izunuma and Uchinuma, and Lake Naganuma) during the winter (Jia *et al.* 2016).

Changes in wintering numbers of Chinese Bean Geese at key wintering sites

Eighteen of the most important key BG wintering sites in the Yangtze River floodplan have been monitored regularly during the non-breeding period from 2003/04 until

Table 5. Annual maximum number of Bean Geese counted at key sites (n = 20) for the two flyway populations in China, during December–February each winter.

ID	Province	Wetlands	2003	2004	2005	2006	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	Maximum
C1	Hunan	East Dongting Lake	17,840	25,825	25,224	10,220	6,853	8,530	18,852	27,966	–	–	–	–	16,813	12,437	21,793	19,070	28,490	28,490
C2		South Dongting Lake	–	1,080	0	–	–	–	–	–	–	–	–	–	0	–	71	308	2,566	2,566
C3		Huanggai Lake	–	–	0	–	–	–	–	–	–	–	–	–	2	–	750	0	2,740	2,740
C4	Hubei	Futou Lake	–	–	0	–	–	–	–	–	–	–	–	–	6,428	–	306	15,021	915	15,021
C5		Wang Lake	–	962	1,650	–	–	–	–	–	–	–	–	–	1,650	–	1,898	2,486	1,177	2,486
C6		Chen Lake	2,850	9,892	10,061	–	–	–	–	–	–	–	–	–	10,434	9,850	5,882	4,585	30,150	30,150
C7		Fu River	–	–	–	–	–	–	–	–	–	–	–	–	3,687	4,400	8,830	4,340	1,189	8,830
C8		Longgan Lake	–	37	6	–	–	–	–	–	–	–	–	–	5,724	2,337	20,585	8,470	13,881	20,585
C9		Tuandun Lake	–	–	–	–	–	–	–	–	–	–	–	–	100	–	185	0	18,500	18,500
C10	Jiangxi	Poyang Lake	–	5,200	16,340	–	–	–	–	–	–	–	–	39,343	38,509	70,990	98,888	135,155	135,064	135,155
C11		Chi Lake	–	–	0	–	–	–	–	–	–	–	–	–	2,392	–	3,169	2,250	2,088	3,169
C12	Anhui	Shengjin Lake	–	2,996	11,233	–	–	41,457	32,210	28,473	43,088	19,005	13,063	25,484	8,714	7,553	12,160	30,455	32,435	43,088
C13		Caizi Lake	–	67	1,605	–	–	–	8,669	22,060	–	–	–	20,889	11,525	1,110	10,948	12,628	6,686	22,060
C14		Huangda Lake	–	4,756	29,838	–	–	–	4,853	3,835	–	–	–	3,457	2,847	8,352	10,632	3	1,105	29,838
C15		Bo Lake	–	2,100	2,065	–	–	–	715	240	–	–	–	0	261	1,600	2,675	2,151	636	2,675
C16		Wuchang Lake	–	26,175	4,750	–	–	–	31,112	4,331	136	4,211	2,784	3,442	4,789	8,666	10,422	6,511	1,825	31,112
C17		Baidang Lake	–	0	0	–	–	–	27	177	754	1,329	3,763	1,141	2,176	57	3,568	974	56	3,763
C18		Shijiu Lake	–	–	–	–	–	–	–	–	–	–	–	–	769	–	3,440	39	74	3,440
C19	Shandong	Yellow River Delta	–	–	–	–	–	–	–	–	–	–	–	5,600	–	–	–	7,600	–	7,600
C20	Hebei	Dongwushi Reservoir	–	–	–	–	–	–	–	–	–	–	–	–	3,441	–	–	–	–	3,441

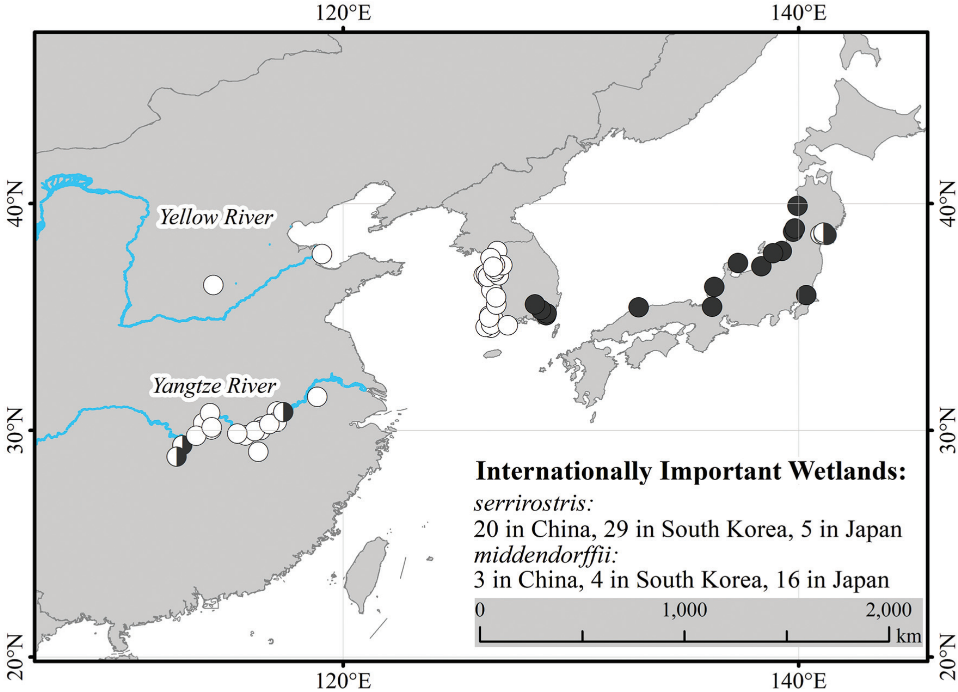

Figure 5. Key wintering sites for Bean Geese in China, South Korea and Japan, based on maximum numbers counted at each site carried out during surveys in winters 2015/16–2019/20 (total 2,531 in China population, 883 in South Korea and 103 in Japan). Black circles = sites used primarily by Eastern Taiga Bean Geese *A. f. middendorffii*; white circles = those used by Eastern Tundra Bean Geese *A. f. serrirostris*; half-black/half-white circles = sites with both subspecies, notably Dongting Lake, Hunan, and Caizi Lake, Anhui, in China, and five marshes in Miyagi Prefecture in Japan (updated from Jia *et al.* 2016).

2019/20 (Table 5). From 2003/04–2019/20, numbers of BG wintering in the Yangtze River floodplain changed before and after 2010, although increasing overall (Fig. 6, Table 6). Four BG key sites (Huanggai, Futou, Chi and Baidang Lakes), held no BG during 2003/04–2004/05 but supported ≥ 1% of the Chinese wintering population during 2018–2020, *e.g.* Futou Lake in Hubei Province peaked at over 15,000 BG in 2019. Intriguingly, 25,825 BG were counted at East Dongting Lake in Hunan Province in 2003/04 compared to 28,490 in 2019/20; these changes contributed to the slight increase of BG counted in Hunan Province. Some 10,061 were counted at Chen Lake in 2004/05, but numbers reached 30,150 in 2019/20, contributing to the overall increase in Hubei Province. Numbers of BG in Shengjin, Caizi, Bo and Baidang Lakes in Anhui Province all slightly increased before and after 2010, while the numbers at Huangda and Wuchang Lakes decreased slightly. Numbers of wintering BG in

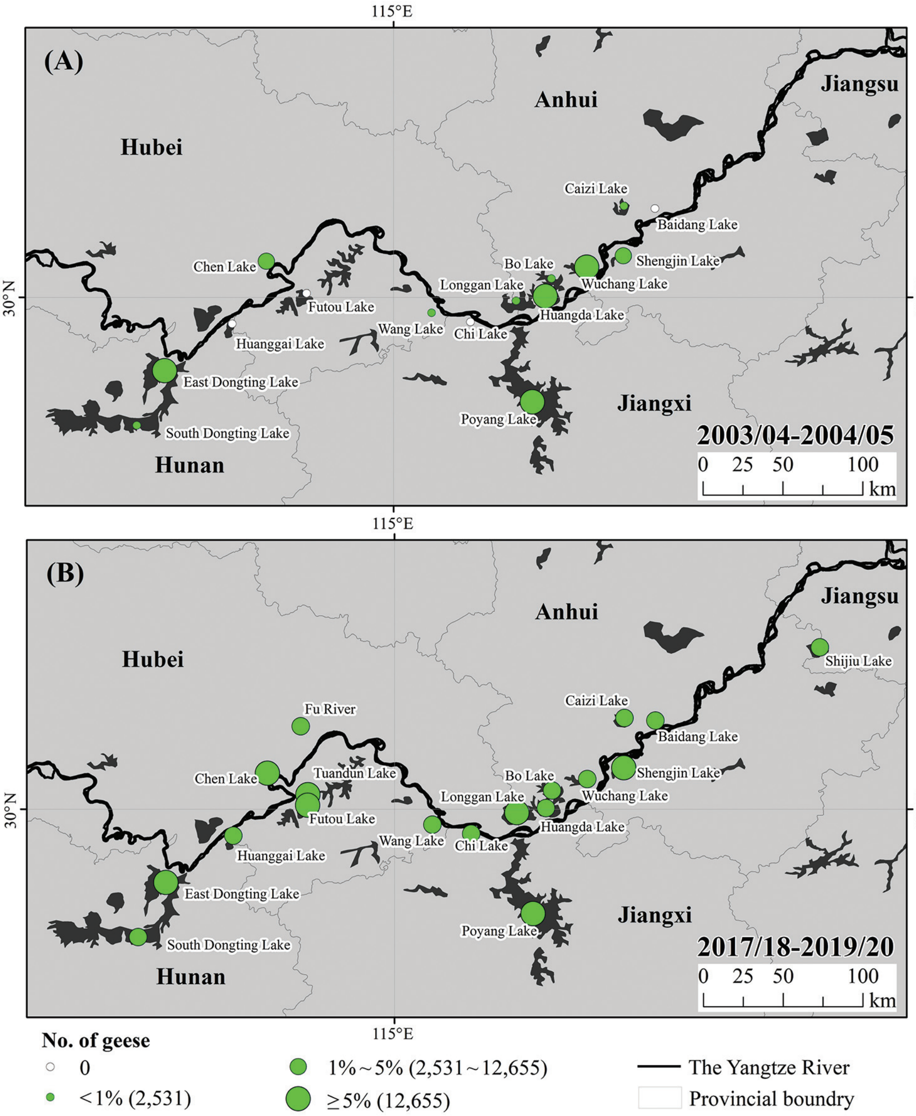

Figure 6. Changes in the maximum number of Bean Geese counted at 18 key sites in the Yangtze River floodplain in China during (A) winters 2003/04–2004/05 (n = 15), and (B) winters 2017/18–2019/20 (n = 18). White circles = zero geese counted; circle sizes indicate numbers counted at the site, as a proportion of the population estimate for China. Three lakes (*i.e.* Fu River, Tuandun Lake and Shijiu Lake) are not shown in A, because there were no survey data from these sites in 2003/04–2004/05. Four lakes (Huanggai Lake, Futou Lake, Chi Lake and Baidang Lake) had no Bean Geese present in 2003/04 and 2004/05, but by 2017/18–2019/20, total numbers were ≥ 1% of the population estimate for China.

Table 6. Summary of the number of survey sites visited at wetlands in the Yangtze River floodplain during six simultaneous surveys (winters 2003/04, 2004/05, 2015/16, 2017/18–2019/20) during December to February, showing the numbers and proportions of Bean Geese counted at each.

Winter	Yangtze River			Wetlands with BG			Total no. of BG
	Total survey sites	Total survey sites with no BG	Total survey sites with BG	Survey sites with < 1% BG	Survey sites with 1–5% BG	Survey sites with ≥ 5% BG	
2003/04	285	219	66 (23%)	57 (86%)	7 (11%)	2 (3%)	79,758
2004/05	346	283	63 (18%)	50 (79%)	10 (16%)	3 (5%)	104,519
2015/16	761	595	166 (22%)	147 (89%)	19 (11%)	0 (0%)	117,561
2017/18	863	643	220 (25%)	192 (87%)	27 (12%)	1 (0%)	206,467
2018/19	1,100	884	216 (20%)	194 (90%)	18 (8%)	4 (2%)	236,788
2019/20	1,079	758	321 (30%)	299 (93%)	18 (6%)	4 (1%)	273,500

Jiangxi Province have increased, especially at Poyang Lake (always one of the major wintering resorts for BG) where wintering numbers reached 135,155 in 2018/19, an increase of 8.27 times compared to those counted in 2009/10. Chi Lake, which held no BG before 2010, has also supported up to 2,392 (2015/16) in years since then.

Discussion

Summer and winter distribution

In this paper, we have attempted to combine satellite tracking data, survey data from various countries, and expert knowledge from the various countries in East Asia to improve our previous knowledge of the breeding and wintering range of BG in East Asia (Fig. 1). Compared to Fox & Leafloor (2018), our data show that the breeding range of the Eastern Tundra BG extends considerably further westwards. The western border of their breeding distribution at the Pyasina River lies very close (*c.* 100 km) to the eastern border of the distribution of the Western Tundra BG, which is considered to be the western Taymyr Peninsula on the eastern banks of the Yenisey River (Heinicke 2018), although the greater part of this population breeds much further west. The close proximity of their ranges, together with the very similar appearance of the Eastern and Western subspecies (D. Solovyeva, pers. comm.), and ring recoveries and reports of Western Tundra BG wintering in East China (Syroechkovskiy Jr 2006), suggests possible overlap in ranges and potential mixing between these populations. A focused genetic study of the two subspecies together with tracking of birds at breeding sites within the potential range overlap in Western Taymyr (Borzhonov 1975; Emelyanov 2000) would help enlighten the extent of overlap between populations and their subspecies status.

While we have relatively little tracking data from Eastern Taiga BG, our migration tracks confirm published distribution data on the relationships between breeding and winter quarters (Fox & Leafloor 2018). As most of our data stem from tracking individuals from very restricted parts of the breeding grounds, we should be very prudent about drawing strong conclusions from so few individuals and sites. Nevertheless, these results together with historical accounts suggest a broader range in the taiga zone across much of southern Siberia, with a discrete population in the mountains of central Kamchatka. Emelyanov (2000) suggested the Altay-Sayan breeding population (which moults in West Mongolia) is isolated from the "main" East-Siberian/ Far-Eastern breeding population by intervening agriculture landscapes which constitute unsuitable nesting habitats for the shy Taiga BG. Unfortunately, our data do not contribute to establishing precisely where the border lies with the breeding distribution of Western Taiga BG. This population is known to breed at least as far as the Eastern part of Yamalo-Nenets Autonomous District in Central Siberia and migrates towards wintering grounds in Xinjiang-Uyghur Province in Western China (Rozenfeld *et al.* 2018). In this respect, we urge that more satellite tracking studies and synchronous winter surveys should be carried out on the Central Asian Flyway, to determine the full relationships between the summering or wintering distribution ranges. We would also urge application of genetic analyses to further verify the division of BG populations in this part of their distribution.

East Asian migration routes

As a result of the large number of satellite tracking studies, we are able to provide here, for the first time, a systematic description of the overall migration connectivity of BG in East Asia, which begins to form a solid basis for delineating flyways.

The GPS-tracked Eastern Tundra BG mostly followed the East Asian flyway, with migration corridors between wintering sites in China, Korea and Japan, and breeding sites which extend from the western Taimyr Peninsula in the west to the Anadyr Region in the east. Additionally, resightings of 492 geese fitted with neck collars have shown that Tundra BG breeding on the Kamchatka Peninsula winter in China and South Korea (Gerasimov *et al.* 2010). Fox & Leafloor (2018) described separate populations of the Eastern Tundra BG on the basis of their wintering areas: in China, Korea and Japan. However, our tracking data showed a complex overlap in migration corridors and breeding ranges, as well as individuals changing between wintering areas in China and South Korea, making shifts between winters as well as using sites in both countries in a single winter. This is further exemplified by northward migration tracks of geese tagged at wintering sites in East China, which fan out over the entire Siberian breeding grounds from the western Taimyr Peninsula to the Anadyr River, while geese tagged at three different sites on the breeding grounds showed connectivity with wintering grounds in Korea and Eastern China.

A migration corridor between wintering sites in Japan and breeding sites in East Russia was confirmed by one individual captured in Chaun Delta. However, given the low sample size and the overlap in breeding range and stopover sites with the population wintering in China and South Korea, we feel that it is prudent to combine these into one East Asian population, although further tracking studies from Japan will be necessary to confirm this.

Taken together, we propose that the Eastern Tundra BG have no clear population structure in China and South Korea and presumably Japan, and geese wintering in all three range states belong to the same population. Interestingly, the lack of a flyway structure for Eastern Tundra BG is in contrast to a clearly delineated structure as found in Eastern Greater White-fronted Goose *Anser albifrons*, despite similar wintering areas and migration corridors (Deng *et al.* 2020).

The flyways of Eastern Taiga BG originated from two differing summer ranges in Sayan and Southern Yakutia, but both populations winter in the Yangtze River floodplain in China. Our tracking data only shows individuals breeding in Yakutia linked to wintering sites in China, but Fox & Leafloor (2018) proposed that the individuals breeding in Yakutia may also winter in South Korea, but alas, these have not been the subject of study. Given the close proximity of the wintering distribution of birds in this flyway, and the lack of tracking data from birds captured in the wintering grounds migrating to Yakutia it is still unclear to what extent there exists exchange between these populations (Roberts *et al.* 2018). We stress the need for more tracking data before we can compile a complete picture of the migration connectivity between breeding grounds and wintering areas of Eastern Taiga BG populations. A larger tracking effort from the wintering grounds might show continuous but parallel migration corridors between wintering grounds in Eastern China and breeding grounds throughout the Siberian taiga. For Taiga BG breeding on the Kamchatka Peninsula, the connection to wintering sites in Japan is well documented by the earlier reports of 77.5% rings out of 731 marked individuals (Gerasimov *et al.* 2010).

Abundance and trends of wintering populations

We here update the estimated wintering abundance of BG in the three management units in East Asia (2012–2019). Because the survey data from China outside the Yangtze River floodplain were not systematic and consistent, they were not included in the population trends analysis of Chinese BG. We hope that in the future, we can strengthen waterbird monitoring to deliver annual coordinated counts from the Yellow River, Huai River and other places, which are known to regularly hold BG.

From 2012 to the present, the population trends of BG in China based on Yangtze River floodplain counts have shown a significant upward trend. A contributory factor could be that in the 2017/18 to 2019/20 surveys, we plotted heat maps of tagged bird densities based on the satellite tracking data of BG on the Yangtze River floodplain, which increased the number of survey sites, and improved the overall survey coverage. However, there is no doubt from regular standardised systematic counts of particular sites, some sites formerly devoid of the species now hold significant numbers of BG and numbers everywhere have increased and have continued to do so. This is consistent with data on a significant increase in the population of geese at the key stopping site in Transbaikalia (52°21'N, 116°5'E) in Russia during the migration from China to the Lena River delta. There was a gradual increase in numbers during the period 2004–2010 and a rapid increase during 2011–2020 (Goroshko 2012). Quite why this should be, when most other Chinese wintering goose populations are declining, is difficult to discern. One potential explanation could be that in the absence of a clear flyway structure, regular exchange of BG wintering in China, Korea and Japan could have occurred, so that despite declines in habitat quality in the Yangtze River floodplain, immigration from increasing populations in Korea and Japan have boosted Chinese numbers. This seems unlikely, since numbers have also increased outside of China, where numbers are modest and too small to explain the increases in Chinese wintering abundance. Other goose species demonstrate more clear population structures, which imply a high degree of fidelity to their wintering grounds and thus different trends in China *versus* Korea and Japan (Deng *et al.* 2020; Ao *et al.* 2020). There is no doubt that with its heavy bill, the BG is a highly flexible herbivore, consuming the above ground green biomass of herbs, grasses and sedges, but also well able to grub in the sediments to retrieve the tough but nutritious below ground storage organs of plants (Zhao *et al.* 2015). It is even able to crack open the leathery and heavily spined fruits of Water Chestnut *Trapa natans* which Swan Geese *Anser cygnoides* cannot (Zhou *et al.* 2010; Carboneras & Kirwan 2019). The species has been shown to switch between different habitats in response to food depletion or availability of new sources of food, while it is also one of the species that exploits agricultural food sources such as winter cereals and harvest remains in China (Zhou *et al.* 2010; Yu *et al.* 2017). The greater foraging flexibility and its willingness to exploit novel feeding opportunities may partly explain the species' success in East Asia. Besides that, contributory reasons for the increase could also lie on the breeding grounds, where a warming climate ameliorates breeding conditions for some species of geese (Nolet *et al.* 2020) with reduced snow cover in spring (Jensen *et al.* 2008) and increases in plant production.

Our tracking reveals a rapid, almost non-stop southward passage over the Russian taiga zone (Wang *et al.* 2018). In autumn, BG migrate at night time at high altitudes, without stopping to rest (Goroshko 2012). In contrast, during spring migration, BG migrate northwards during the daytime, stopping for long periods to refuel and acquire fat stores for 30–40 days at important stopover sites (such as on the Argun River in southeast Zabaikalsky Krai, Russia) before their long uninterrupted flight over the very extensive taiga biome to nesting sites in the northern tundra. Recent effective protection of BG spring staging areas in Zabaikalsky Krai has potentially contributed to increases in abundance among BG using this migration route. Until 2003, BG were very intensively hunted in Transbaikalia where not only were large numbers shot, but hunting disturbance reduced their ability to acquire sufficient energy and nutrient stores for successful migration and investment in reproduction (Madsen & Fox 1995). BG left stopover sites much earlier because of disturbance than is the case now they are protected, suggesting that, historically, geese were unable to establish sufficient stores on these important staging areas. Since 2004, BG hunting has been prohibited in Zabaikalsky Krai, where the main stopover sites are now protected from poachers, and since 2010 the Taiga BG has been included in the Red Data Book of the Zabaikalsky Krai. As a result, numbers of BG staging on key spring stopover sites along the Argun River have increased 6.5-fold during 2004–2020 (from 20,000 to 130,000 individuals; Goroshko 2012; O. Goroshko, pers. comm.).

Wintering BG have been increasing in South Korea since 2005, which is consistent with the results of Kim *et al.* (2016). Syroechkovskiy Jr (2006) reported that this was the result of multiple populations of BG from different breeding areas converging on Korea to winter. Increasing numbers of wintering BG and Greater White-fronted Geese in South Korea coincided with the completion of the Saemangeum seawall project, suggesting that these geese may have benefitted from the creation of large areas of potential feeding habitat in newly reclaimed areas formed along the west coast as novel wintering areas (Kim *et al.* 2016). With the increase in the extent of their preferred habitats in areas not subject to disturbance from human activity and the increase in the population of neighbouring areas (such as China), potentially previously independent wintering populations in China may temporarily join Korean-wintering populations, for which our tracking data provides some evidence.

Numbers of BG wintering in Japan increased slowly up to 1999, before declining slightly in the three years after 2000, but overall numbers have showed a sustained increase since 1970. It has been speculated that a ban on hunting (Miyabayashi 1994), improvement in the quality and quantity of post-harvest food availability on farmland (Shimada 2002) and habitat conservation, could all have contributed to the recovery of the population there (Amano 2009).

Key wintering sites in the three management units

Our study updates information on the key wintering sites for BG in three countries. In China, BG wintering in the Yangtze River floodplain became more widely distributed and increased in number after 2010, which we consider evidence for a genuine and sustained increase in numbers. This corresponds with the significant increase in numbers of BG using key migration stopover sites in Transbaikalia, Russia during 2011–2020. The number of key wintering sites on the Yangtze after 2010 has increased, in comparison with before 2010, with several sites holding increasingly important numbers of BG despite the species being totally absent in earlier years. BG numbers have risen at most of the key lakes, for instance at Poyang, Futou and Longgan Lakes. At Poyang Lake, numbers counted have grown significantly in the winters after 2010, despite the site being not only a strictly protected and well-managed national nature reserve throughout, but subject to good and consistent count coverage. The increase is thought to be at least partially due to (i) increased count effort in inaccessible areas from where telemetry data showed BG to be present, and (ii) artificial feeding of Siberian Crane *Grus leucogeranus*, with the food provided also being exploited by BG.

In South Korea, the distribution of BG is relatively concentrated, and the increase in population is mainly reflected in the increase at key sites. This seems likely to be associated with the obvious changes in the degree of availability of suitable habitats in coastal areas of South Korea in recent years, from the original intertidal habitats to highly productive agricultural land where BG can benefit from agricultural subsidies (Kim *et al.* 2016).

BG show a scattered distribution in Japan, but they are mainly found near rivers, lakes and surrounding farmland. In recent years, the number of BG at key wintering sites in Japan has increased. Throughout the long period of standardised waterbird counts, the number and distribution of key sites for BG has not changed in Japan. Therefore, the increase in wintering numbers of BG there is likely a response to an increase in the extent and/or quality of suitable habitats, potentially aided by increased reproductive success on the breeding grounds (for example observed in West Chukotka; D. Solovyeva, unpubl. data) in response to climate warming and increased vegetation productivity in the arctic. At present, we have little knowledge about differences in habitat use between both subspecies in Japan. For this reason, it would be desirable to analyse habitat selection by BG in Japan (as already undertaken in South Korea and China) through tracking and remote sensing data, to describe their interactions with the farmland and wetland ecosystems they exploit. Such information would provide the potential to improve feeding opportunities in their respective wintering landscapes and effectively manage and conserve the geese while avoiding potential agricultural conflict.

Conservation and research recommendations

The BG is a widely distributed species in East Asia and this study has shown how much more we have come to understand about the population in the past decade. However, we still lack vital information about the true extent of the breeding and wintering areas and the migration routes that link these, especially for Tundra BG wintering in Japan and for the "main" population (East Asian Continental flyway) of Taiga BG.

In assessing the rate of change in numbers of BG wintering in China, this study was able only to estimate the annual numbers and trends in abundance for BG in the Yangtze River floodplain. We need to extend systematic monitoring to include all sites used by the species wintering in the Yellow River Basin and Xinjiang Province (and potentially elsewhere), to obtain more accurate data on population sizes and trends in China. In order to clarify the distribution and abundance of the different BG subspecies, it is essential to undertake field surveys that take care to discriminate and determine the numbers of each of the four subspecies present throughout the wintering range.

In this analysis, we have not presented data to identify key staging areas, which are potentially a critical element for all flyway populations, enabling geese to top up depleted energy reserves along their migration corridors. Establishing the relative importance of these areas is a critical goal for the future. To understand the full extent of the BG distribution in East Asia, its flyway population structure and the key sites they depend upon, it is necessary to establish an effective monitoring programme to track annual population trends, which requires Russia, Mongolia, China, South Korea, Japan and other East Asian countries to work jointly on a long-term scientific research and monitoring programme.

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