Migration strategies of Swan Geese *Anser cygnoides* from northeast Mongolia

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Abstract

In 2006–2008, 25 Swan Geese *Anser cygnoides* were marked with solar-powered GPS satellite transmitters in northeast Mongolia to examine the timing and pathways of their migration. Most geese began their autumn migration in August, flying southeast toward a staging area at the Yalu River Estuary on the China-North Korea border. After staging for several weeks, the Swan Geese continued to their wintering grounds at wetlands along the Yangtze River Basin of eastern China in December. Spring migration commenced in late February, and the birds following either a same-route or loop migration to arrive at the breeding grounds in mid April. Swan Geese used a larger number of staging areas for a longer duration when they were north of 42°N latitude; they seemed to avoid staging for extended periods in the highly urbanised areas of eastern China. Further research should examine threats and disturbances to the geese in relation to human population growth and increasing urbanisation.

Key words: *Anser cygnoides*, East Asian Flyway, migration, satellite telemetry, Swan Goose.

Understanding local movements and migration across large landscapes is critical for identifying the factors that influence the survival of migratory birds and for devising effective conservation strategies (Berger 2004; Newton 2007). Migration data provide insights into specific areas used, migratory connectivity, timing, stopover sites, migratory behaviour and physiology (Berthold *et al.* 2003; Robinson *et al.* 2010). In addition, use of satellite tracking data has improved our understanding of the ecology of diseases such as avian influenza and the connectivity between outbreak areas and wild bird locations (Gaidet *et al.* 2010; Newman *et al.* 2009; Takekawa *et al.* 2010).

The Swan Goose *Anser cygnoides* is a globally threatened species listed as "vulnerable" in the latest Red List of Threatened Species of the International Union for Conservation of Nature and occurs only in East Asia (BirdLife International 2009). Recent counts made both at the breeding grounds in Mongolia and Russia (Goroshko 2003; Goroshko *et al.* 2004; Tseveenmyadag *et al.* 2007) and at wintering sites in China (Zhang *et al.* 2010) indicate a dramatic decline in numbers which has been attributed to: drought-induced wetland loss, disturbance of nesting birds by livestock, competition with livestock for grazing areas, illegal hunting, egg collection, reduction in the abundance of submerged vegetation (*i.e.* the birds' food supply) due to water pollution and dam water regulation, and wetland conversion for agriculture and development projects (Goroshko 2003; Goroshko *et al.* 2004; Poyarkov 2001; Poyarkov 2006; Tseveenmyadag *et al.* 2007; Zhang *et al.* 2010; Fox *et al.* 2011). The decreasing population size may also be related to habitat change or degradation at stopover sites along the migration flyway. Furthermore, the highly pathogenic avian influenza H5N1 virus, which has been reported across the Swan Goose wintering range, poses a significant threat to this species.

In 2006 and 2008, moulting geese were fitted with satellite transmitters and tracked from their breeding sites on the Mongol Daguur in northeast Mongolia to their wintering grounds in the Yangtze River Basin of eastern China. Global positioning system (GPS) location data were used to describe their annual migration in detail, including identifying stopover and wintering sites, documenting the timing of migration, and delineating migration corridors along the East Asian Flyway. In addition to providing the first documentation of the complete migration cycle of the Swan Goose, a major focus of this study was to determine how the birds used the landscape in relation to human populations. We hope that the greater knowledge and understanding of how Swan Geese use the landscape, provided by tracking the movements of individual birds, will help to improve the prospects of conservation efforts directed at this species.

Study area and methods

The Mongol Daguur region can be characterised as a vast temperate grassland steppe, with low mountains and rolling hills, and with numerous small and medium sized steppe lakes and wetlands. Nomadic herders and their livestock are the main populations in the area. Most lakes in this region are fed by rain water; only a few are fed by running rivers and streams. The lake and wetland steppe landscape extends north into neighbouring Russia and east into China; this border region of the three countries is an important area for the Swan Goose and many other wetland-dependent species in northeast Asia (BirdLife International 2005).

Swan Geese were captured during their moulting period by herding them into a drive-trap or by capturing them in dip-nets from boats. A total of 25 Swan Geese were caught at the Khaichiin Tsagaan Lake (49.683°N, 114.684°E) in the Mongol Daguur of northeast Mongolia in July 2006 (Fig. 1), and a further 41 geese at Khaichiin Tsagaan Lake, Khorin Tsagaan Lake (49.661°N, 114.606°E), and Khokh Lake (49.540°N, 115.585°E), in the same region of northeast Mongolia, in 2008. All captured geese were tested for the avian influenza virus, but none were found to be positive (authors' unpubl. data). Geese were measured and marked with aluminium metal leg rings and plastic neck collars for individual identification, using orange neck collars with black alphanumeric codes (with one letter and two numbers) in 2006 and green neck collars with white alphanumeric codes in 2008.

We fitted 45 g or 70 g solar-powered Argos-GPS platform transmitter terminals (PTTs: Microwave Telemetry, Inc., Columbia, MD, USA) to the backs of selected adults, using a teflon-ribbon harness (Bally Ribbon Mills, Bally, PA, USA). Ten 70 g transmitters were fitted in 2006 and fifteen 45 g transmitters in 2008. Backpack harnesses for the transmitters were reinforced to prevent loss, because Swan Geese have very strong bills and their lower mandibles are serrated for cutting plants and grasses. The weight of the transmitter and harness was < 3% of the birds' body mass. Birds were released as soon as possible after marking, typically within an hour, back at their capture locations. Procedures for capture, handling and marking were reviewed and approved by the U.S. Geological Survey Patuxent Wildlife Research Center Animal Care and Use Committee, and also by the University of Maryland Baltimore County Institutional ACUC (Protocol EE070200710). Transmitters were programmed to record GPS locations every 2 h and Argos locations downloaded every 2–3 days. Only geese that had complete migration routes were included in analyses, and only GPS data were used, which are typically accurate to distances of < 10 m.

The annual cycle of the Swan Goose was divided into five different periods: 1) autumn (southbound) migration, 2) wintering, 3) spring (northbound) migration, 4) breeding season, and 5) moulting or post-breeding. We examined the location data and used specific areas, duration of stay, and scale of movements to estimate the duration of these periods. Movement from the moulting and wintering areas was used to indicate the onset of migration. Geese were classified as breeding if the GPS fixes were found to be in very close proximity to each other at a site over more than a one-week period during the breeding season (Ely *et al.* 2007). The arrival time was defined as the first date that Swan Geese were detected on the breeding grounds. Swan Geese prefer to use larger lakes for moulting because they provide more safety when flightless (authors' pers. obs.). We assumed that movements of several kilometres from breeding areas on smaller lakes to larger lakes indicated that the birds had moved to moulting grounds. Staging areas, where migrating birds store fuel for migration, were identified as sites where birds remained in the vicinity (*i.e.* no large-scale movements to or from the site occurred) over a period of ≥ 7 days during the migration period (Warnock 2010). Visual inspection of locations in close proximity and limited movements at the southern end of the migration were used as cut-off dates for the autumn migration and to determine arrival at the wintering grounds (Oppel *et al.* 2008).

Various factors such as food supply, local environment, weather, proximity to main wintering areas, and hunting pressure may disturb and eventually influence the timing of bird migration (Berthold *et al.* 2003). In this study, the linear distance from stopover locations to the nearest urban area was used as an indicator of potential disturbance to Swan Geese along the migration route (Benitez-Lopez *et al.* 2010). Furthermore, we examined the flight speeds and distances travelled by birds between consecutive locations to see whether flights north and south of 42°N differed significantly, with the density of urban areas in the Swan Goose flyway generally being higher south of this latitude (Fig. 1). A Wilcoxon signed-rank test was used to test whether there was a significant difference in the average speeds and flight distances recorded for individual birds during spring and autumn migration. Analyses were conducted and box plots produced using R statistical software (R Development Core Team 2011). Mean flight duration and distances are given with s.d. values throughout.

The European Space Agency's GlobCover land cover map with 300 m spatial resolution (Bicheron *et al.* 2008) produced for the period December 2004 – June 2006 was used to determine land cover types at stopover and staging locations along the Swan Goose migration route in East Asia and for calculating distances between towns or villages and stopover locations. Location data were plotted within ArcGIS 9.3 (ESRI 2008) to determine the migration route and stopover sites, and to calculate the flight distances of Swan Geese. The 50%, 95% and 99% fixed kernel home ranges were calculated using Hawth's Analysis Tools (Beyer 2004) in ArcGIS 9.3 to determine the areas used by Swan Geese staging at the Yalu River Estuary (39.869°N, 124.301°E) and wintering at Poyang Lake (29.217°N, 115.960°E), including defining the boundaries of movements by individual geese in these areas.

Results

Ten geese were fitted with satellite transmitters in 2006 and 15 geese in 2008. Overall, 17 (68%) birds provided satellite tracking data useful for evaluating migration. Fourteen of the useful tracks were from the 2008 deployment, but only three of 10 geese from 2006 yielded data. Although the other seven birds appeared normal upon release, they did not swim well, and five were recaptured by the next day. We found that they had been adversely affected

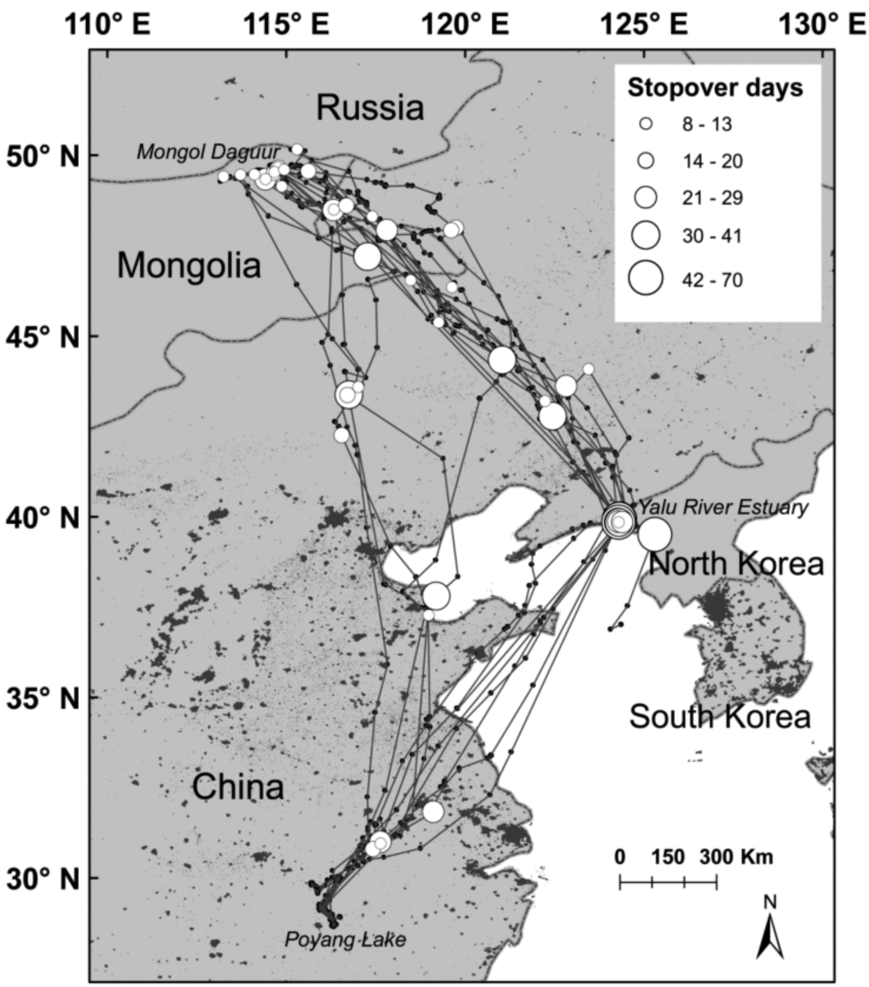

Figure 1. Migration paths, locations, and important stopover sites of Swan Geese marked with satellite transmitters in northeast Mongolia. Swan Geese were captured at the Mongol Daguur, and many used the Yalu River Estuary as a major staging site. Poyang Lake was the main wintering area along the Yangtze River Basin. White circles = major stopover locations; black shading = urbanised areas.

by capture myopathy, because for short periods they had entangled their wings or feet in the small-mesh fishing net used as a holding pen that year (a different type of holding pen was used in subsequent years).

A total of 15,458 GPS fixes were obtained with an average of 858 locations per individual, ranging from 14–2,420 locations per bird. Such large individual variation was influenced primarily by the duration over which signals were received

Table 1. Morphological data for Swan Geese fitted with satellite transmitters and a summary of the performance of the transmitters.

Satellite ID	Sex	Age	Weight (g)	Culmen (mm)	Tarsus (mm)	Start date of transmission	Date last signal received	Total days with signals	Total number of GPS fixes
67578	F	Ad	3550	40.5	835	30-Jul-06	17-Sep-06	50	378
67585	F	Ad	2600	–	986	30-Jul-06	13-Nov-07	472	1618
67697	F	Ad	2500	–	–	30-Jul-06	30-Nov-06	124	721
82101	F	Ad	2700	98.6	84.5	29-Jul-08	2-Dec-08	127	811
82102*	M	Ad	2900	103.4	89.6	29-Jul-08	4-Nov-08	99	14
82103	F	Ad	2920	84	81.9	27-Jul-08	9-Dec-08	135	437
82104	M	Ad	3800	89.2	92.6	27-Jul-08	24-Aug-08	29	134
82105	F	Ad	3490	95.3	91.5	26-Jul-08	18-Aug-09	389	2,302
82106	F	Subad	2550	84.7	75.4	27-Jul-08	27-Sep-08	63	418
82107	F	Ad	3100	90.5	80.5	27-Jul-08	27-Nov-09	489	1,534
82108	F	Ad	2850	92.7	79.9	27-Jul-08	18-Aug-09	388	2,420
82109	M	Ad	3150	89	84.6	27-Jul-08	23-Sep-08	59	468
82110	M	Ad	1700	89.9	80.5	27-Jul-08	20-Dec-08	147	314
82111	F	Ad	2750	88.2	75.8	27-Jul-08	13-May-09	291	1,954
82112	M	Ad	–	80.7	77.7	27-Jul-08	10-Dec-08	137	1,100
82113	F	Ad	2720	88.1	80.5	27-Jul-08	5-Nov-08	102	306
82114	M	Ad	2700	83.8	76.4	29-Jul-08	5-Sep-08	39	227
82115	M	Ad	3100	55.4	50.3	27-Jul-08	3-Sep-08	39	302

*Not included in the analysis

Table 2. Chronology and movements of satellite-tracked Swan Geese during their annual cycle.

Migration periods	**Autumn migration**	**Winter**	**Spring migration**	**Breeding**	**Post-breeding**
No. of geese tracked	17	5	5	5	3
Start or arrival date (range)	3 Aug–16 Sep	23 Oct–1 Jan	25 Feb–5 Apr	13 Apr–4 Jun	16 Jun–22 Jun
Start or arrival date (median date)	8 Aug	7 Dec	14 Mar	9 May	21 Jun
Min–Max duration (days)	74–146	56–155	30–66	43–70	61–65
Average duration ± s.d. (days)	107 ± 29	104	52 ± 15	53	63
Linear distance travelled (km)	2,580–3,170	–	2,570–2,700	–	–
Average linear distance travelled ± s.d. (km)	2,900 ± 272	–	2,630 ± 54	–	–

(range = 29–489 days; Table 1). Departure from the post-breeding area was documented for 17 birds, five of which provided complete autumn and spring migration histories, and twelve birds had partial migration histories. Two geese with working transmitters made autumn migrations in the second year after capture. All birds migrated within the East Asian Flyway.

Autumn migration

The route and timing of the autumn migration was documented for six male and eleven female geese (Table 2). Autumn migration started between 3 August and 16 September (median date = 8 August, n = 19). Most birds started their migration in August, but two birds (transmitter numbers 82103 and 82108) started in September in 2008. Signals for five birds (#67578, 82104, 82110, 82114 and 82115) that started their autumn migration ended before reaching the Hinggan Mountains in Inner Mongolia, China. Ten Swan Geese progressed across eastern Mongolia and the Manchurian Plain to the Yalu River Estuary on the border of China and North Korea, but from here they flew southwest to wintering areas in east China. Two Swan Geese migrated to areas at the same latitude as the Yalu River Estuary but flew directly south to the wintering grounds (#67585, 82113).

The Yalu River Estuary on the border between China and North Korea was a key staging area for Swan Geese (Figs. 1 and 2a). Two birds tracked in 2006 arrived after mid October, whereas five birds tracked in 2008 arrived at the end of September, and two arrived around at the end of October. All birds stayed at this staging area until the end of December when air temperatures sharply decreased and freezing conditions likely reduced availability of food resources. The 99% fixed kernel home ranges for Swan Geese in this location during the autumn and spring migration were 176 km^2 and 190 km^2, respectively.

Swan Geese arrived at the wintering grounds in December, although one bird arrived on 1 January (Table 2). Five birds (#67585, 82105, 82107, 82108, and 82111) that successfully completed the southbound migration travelled 2,580–3,170 km (mean = 2,900 ± 272 km, *n* = 5) to reach their wintering grounds in eastern China. Autumn migration for these birds took 74–146 days (mean = 107 ± 29 days, *n* = 5). Individual variation in the autumn migration period was largely due to the different length of time geese spent at the staging areas.

Wintering

Poyang Lake, located in the Jiangxi Province along the Yangtze River and the largest freshwater lake in China, was an important wintering area for the Swan Geese tracked from northeast Mongolia (Fig. 2b). Four geese (#67585, 82105, 82107 and 82111) arrived first at the northwest region of the lake. Later, geese moved to the south of the lake for most of the remaining wintering period and returned to the northwest just before the spring migration began. Another goose (#82108) spent the winter at Fengsha Lake (30.927°N, 117.630°E) in Anhui Province located within the Yangtze River Basin 240 km northeast of Poyang Lake and known to be another important wintering site for Swan Geese (Fox *et al.* 2008). Arrival dates at wintering areas ranged from 23 October to 1 January with a median date of 7 December (*n* = 5). Swan Geese spent 56–155 days (mean = 104 ± 37 days) at the wintering grounds. The 50%, 95%, and 99% fixed kernel home range of Swan Geese in this location during their winter stay were of 60 km^2, 370 km^2 and 580 km^2, respectively (Fig. 2b).

Spring migration

Swan Geese departed for their spring migration between 25 February and 5 April (median = 14 March, *n* = 5 birds). Northbound travel lasted for 30–66 days with an average of 52 days (s.d. = 15 days). The spring migration routes for three of the Swan Geese were similar to those taken during the autumn migration. Two geese followed different routes, flying directly to the north without staging at the Yalu River Estuary. Geese which followed a same-route spring migration took 30–66 days to reach the breeding grounds, with many shorter stopovers between staging areas, whereas the two geese following a loop migration travelled for 43 and 60 days respectively, differing from geese following the same-route migration by having longer non-stop flights with fewer staging periods. The five geese completed the spring migration after travelling 2,570–2,700 km (mean = 2,630 ± 54 km) to reach the breeding grounds in northeast Mongolia.

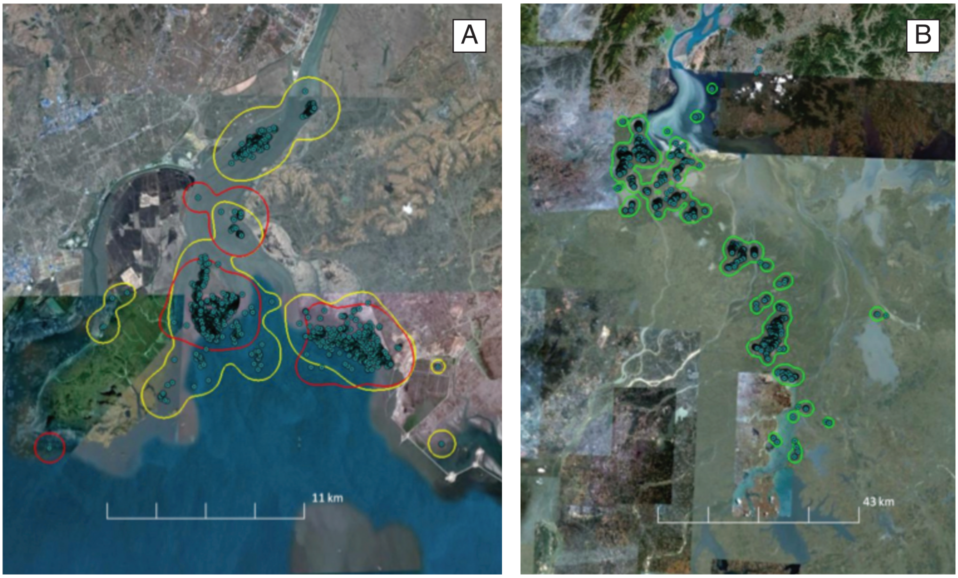

Figure 2. Foraging and roosting locations of Swan Geese at major staging and wintering areas. Contours represent 99% fixed kernel home ranges in three different seasons. Yellow contours show areas used during autumn migration (September–December), red contours indicate spring migration locations (March–April), and green contours show wintering locations (January–February). Blue dots shown are locations for five birds that made a complete migration cycle. **A.** Yalu River Estuary at the border area between China and North Korea. **B.** Poyang Lake, Jiangsu Province, China.

Arrival at breeding and post-breeding areas

The first bird arrived at the breeding grounds on 13 April and the last arrived on 4 June (median = 9 May, n = 5). The geese stayed on the breeding grounds for 43–70 days (mean = 53 ± 15 days). Four birds arrived at the same area where they were captured in the previous year, the fifth (#82105) probably bred at Tsagaan Lake (47.911°N, 119.604°E) in China. Swan Geese arrived at their moulting sites between 16–22 June. Post-breeding areas where geese typically moult were on lakes with grassy meadows. Swan Geese remained at these post-breeding areas for two months prior to the beginning of autumn migration in August. Two birds were tracked on a second autumn migration beginning on 23 August 2007 (#67585) and on 18 August 2009 (#82105). Migration routes of these birds were similar to the previous year up to the time their transmitter signals ended in mid migration.

Staging areas

A total of 54 staging areas were used by the 17 Swan Geese after they left the breeding and moulting grounds. Five female Swan Geese that had complete migration cycles had similar numbers of stopover areas during the migration (ANOVA test: $F_{4, 49}$ = 0.17, P = 0.95, n.s.). The number of staging areas where birds spent on average more than 10 days ranged from 4–9 sites per bird. Birds were spending 8–70 days per site (mean = 23 days; 95% UCI = 41, LCI = 4). We also obtained detailed information on location and habitat for selected major staging and stopover sites (Table 3).

The Yalu River Estuary was a key staging area or pre-wintering area. Eight Swan Geese spent 16–70 days there (mean = 34 days) from 16 September to 20 December. The Swan Geese did not use adjacent agriculture fields to forage during this period. Instead, they used mostly mud flat areas and habitats along the coastline (Fig. 2a).

In general, the number of stopover and staging areas and the duration Swan Geese spent at important staging areas were greater when geese were north of 42°N (Fig. 1). There was some preliminary evidence that the distance from a stopover location to urban areas decreased as the birds flew south, with the smallest distances involved being close to the wintering grounds (Fig. 3). Few Swan Geese used Buir Lake, which is one of the largest lakes in the region, as a stopover site, although 24,000 Swan Geese have been recorded there previously (Goroshko 2004). Only one of our marked geese stopped at this lake, for 1–2 days during autumn migration. There were no obvious major changes in flight speed and distance during migration along the direct route (Fig. 4).

Seventy-eight locations were useful for estimating flight speeds and successive distances during migration. Overall, the Swan Geese migrated on average at 31 ± 1.8 km/h (n = 78; range = 11–77 km/h for individual flights), at 31 ± 2.2 km/h in autumn (n = 38; range = 12–66 km/h) and at 32 ± 2.8 km/h in spring (n = 40; range = 11–77 km/h for individual flights). A Wilcoxon signed-rank test found no significant difference in average flight speeds recorded during the autumn and spring migration (Z = –0.24, P < 0.82, n.s.). The average distance travelled by individual birds also did not differ markedly between autumn and spring (Z = 0.37, P < 0.72, n.s.) (Fig. 4). Non-stop flights of > 24 h duration were observed for three occasions, when geese with transmitters #82105, #82107 and #82111 flew for 26, 29 and 30 h in September and December 2008. These flights were of 977 km, 1,053 km and 1,395 km, at speeds of 38, 36 and 47 km/h respectively.

Discussion

Two distinct flight paths were used during autumn migration by the Swan Geese tracked in our study: 1) an indirect flight between Mongol Daguur in northeast Mongolia and Poyang Lake in eastern China through the Yalu River Estuary on the China-North Korean border, and 2) a direct flight between the Mongol Daguur and the Poyang Lake. Geese flying through the Yalu River Estuary during their migration flew more than 300 km farther than those flying straight from the Mongol Daguur to Poyang Lake, but more marked geese used this route. In terms of maximising energy and minimising time, migration along this pathway appears more costly than the direct flight. Many migratory species make detours to avoid hazardous and inhospitable land

Table 3. Location, habitat, and duration of stay of Swan Geese at selected major stopover sites (*i.e.* where birds spent on average more than 10 days). After moulting, geese spent over a week at 54 different migration locations.

Country	Location	Coordinates	Habitat	Season	Date	Number of PTT marked birds	Average Days	Range
Mongolia	Khavtsgait Lake	N 49.347° E 114.416°	Lake	Autumn	13 Aug–3 Sep	1	22	22
Mongolia	Shandin Lake and Kherlen River	N 48.504° E 116.333°	Lake and riparian meadow	Autumn	25 Aug–24 Sep	6	10	2–18
Mongolia	Olziitiin Shavar Lake	N 47.200° E 117.275°	Lake and riparian meadow	Autumn	15 Sep–10 Oct	1	26	26
China	Bayan Hushu Lake	N 47.913° E 119.606°	Lake	Autumn	10 Sep– 6 Sep	1	17	17
China	Dalai Hu Lake	N 43.377° E 116.705°	Lake	Autumn	10 Sep–12 Oct	2	20	13–27
China	Ajila Gacha Lake	N 44.331° E 121.065°	Small lakes	Autumn	22 Sep–2 Nov	2	10	8–13
China	Sulishi Lake	N 42.795° E 122.439°	Small lake	Autumn	20 Sep–23 Oct	1	34	34

Table 3 *(continued)*

Country	Location	Coordinates	Habitat	Season	Date	Number of PTT marked birds	Average Days	Range
China	Huojia Lake	N 43.628° E 122.817°	Small lake	Autumn	8 Oct–5 Nov	1	27	27
China and North Korea	Yalu River Estuary	N 39.869° E 124.301°	Estuary	Spring	15 Mar–14 Apr	2	22	19–26
				Autumn	16 Sep–20 Dec	8	34	16–70
North Korea	Changp'o	N 39.530° E 125.367°	Seashore	Autumn	1 Oct–4 Dec	2	38	13–63
China	Yellow River delta	N 37.809° E 119.185°	Seashore	Autumn	4 Oct–5 Nov	1	30	30
China	Chishan Lake	N 31.824° E 119.096°	Ponds and irrigation channels	Autumn	6 Dec–30 Dec	1	24	24
China	Chenyao Lake	N 30.939° E 117.624°	Lake	Autumn	26 Nov–9 Dec	1	14	14

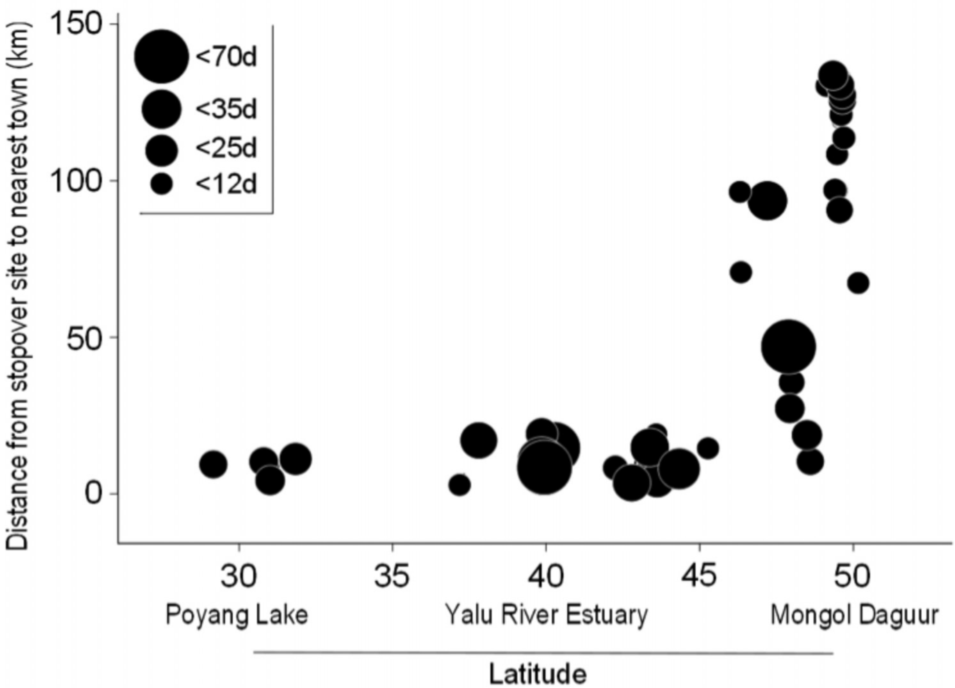

Figure 3. Changes in linear distance from stopover sites to the nearest urban area in relation to latitude (n = 5 birds). Size of the dark circles indicates the duration of stay (in days) at stopover sites; each circle represents a location and duration is illustrated in the legend.

masses or water bodies, and thus reduce the risks encountered during migration (Newton 2007). However, there are no major physical barriers such as a large mountain range or body of water that would prevent Swan Geese flying directly south to Poyang Lake from Mongolia. In fact, geese flying to the Yalu River Estuary must cross Bohai Bay en route to the Yangtze River Basin.

One possible explanation for the intensive use of this estuary by Swan Geese is that weather and climate patterns influenced their migration (Gordo 2007). Prevailing winds and favourable conditions may favour stopovers by migratory birds along the Yellow Sea (van de Kam 2010). Alternatively, the Swan Geese may have been avoiding interior areas with highest densities of human, agriculture, and infrastructure development while exploiting natural areas as much as possible before arriving at Poyang Lake. Furthermore, flying via Yalu River could be a traditional migration route to Japan and South Korea where Swan Geese commonly used to winter (Brazil 1991).

Swan Goose migration between the Yalu River Estuary and Poyang Lake was brief, with fewer stopovers compared to flights

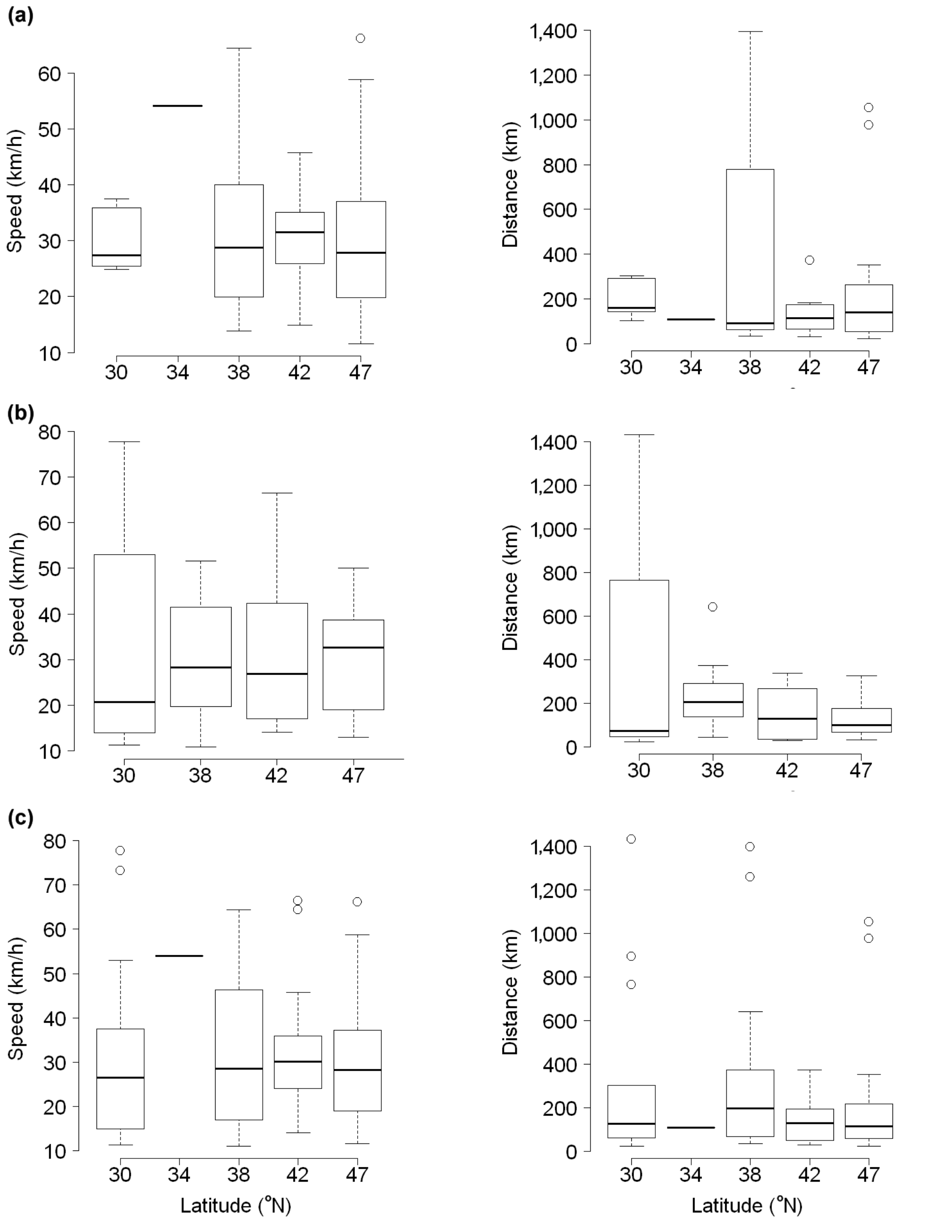

Figure 4. Consecutive flight distance and groundspeed of migration for Swan Geese relative to breeding and wintering locations (latitude). Latitude is represented by the midpoint of 4 degree intervals on the x-axis. Outliers indicate the ability of some individuals to cover long flight distances at rapid speeds during non-stop flights. Seasons are indicated as (a) autumn migration, (b) spring migration and (c) both seasons combined.

between Mongol Daguur and the Yalu River Estuary. In general, we did not see major changes in average flight speeds and distances along the migration route in autumn and spring (Fig. 4), although there were some substantial maximum groundspeed and flight distances recorded during autumn migration prior to the geese arriving on the Yalu River Estuary. The data show that Swan Geese can cover c. 1,400 km within 30 h, but the ecological and environmental factors influencing such flights are not known.

Availability of stopover sites and duration of stay are important parts of the annual cycle and influence birds' migration strategies (Berthold *et al.* 2003; Newton 2007). Marked Swan Geese made more stopovers in the areas north of 42°N latitude, which may indicate the presence of more suitable sites in the north that were primarily natural wetlands. There are currently few large human concentrations in the areas intersecting northeast Mongolia, Russia, and China where Swan Geese breed and moult. Thus, the region is mostly undisturbed or underdeveloped. Swan Geese exhibited longer stopover durations in the north of 42°N latitude during both the autumn and spring migration. Furthermore, our data suggest that the proximate distance from a stopover location to urban areas decreased as birds flew south, and the distance was least near the wintering area (Fig. 3). Swan Geese may prefer to use landscapes with lower human densities and less urbanisation while exploiting areas with rich in food supply.

The scale of urbanisation in eastern China, home to 10% of the world's population (van de Kam 2010) and the majority of the population in China, is very intensive. As a result, human development has dramatically changed land cover and land use practices in eastern China (Deng *et al.* 2008). Avian species often respond dramatically to urbanisation and development depending on spatial scales and local food, available habitats, and disturbance levels (Clergeau *et al.* 1998; Garaffa *et al.* 2009; Klein 1993; Marzluff 2001; Traut & Hostetler 2003). Large scale changes at a landscape level in east China may have affected migratory behaviour of the Swan Geese historically, but there are too few historical data available to analyse this hypothesis.

Nonetheless, eastern China is the most important wintering area for the Swan Goose, and nearly 95–100% of the geese from the Dauria region are found wintering there (Cao *et al.* 2008a; Zhang *et al.* 2010). In the last four decades, the wintering range of Swan Geese has gradually contracted coincident with a decline in their populations likely related to increased poaching, water-level control for irrigation and industrial use, habitat degradation of coastal and inland wetlands, and pollution (Barter *et al.* 2007; Cao *et al.* 2010; Quan *et al.* 2002; Zhang *et al.* 2010). Expansion of urbanisation and economic development in east Asia has caused large-scale change in ecosystems of the region. Also, degradation of wetlands in eastern China has contributed to distribution range shifts, contraction, and northward expansion for many waterbird species (Cao *et al.* 2008b; Cao *et al.* 2010; de Boer *et al.* 2011).

Extensive use of mud flats by Swan Geese has been documented during the non-breeding season. Swan Geese were commonly observed grubbing on underground rhizomes of *Vallisneria asiatica* in mud flat habitats at wintering sites in Shengjin Lake (Fox *et al.* 2008; Zhang & Lu 1999) and in the Han River Estuary (Han *et al.* 2003). It is unclear what constitutes the main food supply for staging Swan Geese in the Yalu River Estuary mud flats and why geese do not use grassland habitats and agricultural fields. However, it could be related to the availability of foraging habitats in that region and easy access to nutrient-rich food.

In addition, Poyang Lake is one of the major wintering areas for the Swan Goose and many other waterbirds but has been called the potential epicenter of HPAI H5N1 (Cao *et al.* 2008a; Prosser *et al.* 2009; Takekawa *et al.* 2010). Outbreaks of highly pathogenic avian influenza H5N1 have occurred along the migration route from northeast Mongolia through the Yalu River Estuary to Poyang Lake (Sakoda *et al.* 2010; Takekawa *et al.* 2010). The density of wetlands along this migration route is sparse in northern compared to southern regions where man-made wetlands are abundant (Bicheron *et al.* 2008). Thus, in stopover areas north of 42°N, Swan Geese may have greater chances of interactions with waterbirds originating from different parts of south and east Asia, increasing the potential for H5N1 transmission. Consequently, potential spread and persistence of HPAI H5N1 in this region may pose a threat to the Swan Goose population.

It remains unclear whether the migratory pathway we documented through the Yalu River Estuary is a historical or recently-developed route that arose in response to land use and land cover changes in eastern China. However, Takekawa *et al.* (2010) report that several different duck species, migrating from Poyang Lake to northeast China and eastern Russia in the spring, made extensive use of the region as a staging area, as do many shorebirds (van de Kam 2010). Thus, if we wish to conserve stopover sites along routes for migratory bird species in east Asia, obtaining a better understanding of the effects of urban area expansion and development at key stopover sites such as the Yalu River Estuary is crucial. Those impacts may be most visible for species with larger body size and narrow habitat niches such as the Swan Goose.

Acknowledgements

This work was funded by the U.S. Geological Survey (Patuxent Wildlife Research Center, Western Ecological Research Center, Alaska Science Center, and Avian Influenza Program), the United Nations Food and Agriculture Organization, Animal Production and Health Division, EMPRES Wildlife Unit. The field work of Mongolian and Korean researchers in 2006 was funded by the Cultural Heritage Administration of Korea through Korean-Mongolia Joint Swan Goose Research Project. The data analysis was supported by a grant from the U.S. National Science Foundation EPSCoR programme (NSF-0919466). We are grateful to Sabir Bin Muzaffar, Eric Palm, David Douglas, Bill Perry (U.S. Geological Survey), Taej Mundkur (Wetlands International), Martin Gilbert (Wildlife Conservation Society), Paek Won Kee, Chun Byung Sun (Korean National Science Museum), and the staff of the Wildlife Science and Conservation Center of Mongolia for their assistance. The Ministry of Nature and Environment of Mongolia provided permission to capture and satellite-tag Swan Geese through the Institute of Biology, Mongolian Academy of Sciences. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

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Photograph: Swan Geese grazing and sleeping. Photograph courtesy of the WSCC of Mongolia.

Photograph: Swan Geese in flight over the Mongol Daguur. Photograph courtesy of the WSCC of Mongolia.