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Migration through the Eastern Palearctic (EP) flyway by tundra swans (*Cygnus columbianus*) has not been thoroughly documented. We satellite-tracked the migration of 16 tundra swans that winter in Japan. The objectives of this study were 1) to show the migration pattern of the EP flyway of tundra swans; 2) to compare this pattern with the migration pattern of whooper swans; and 3) to identify stopover sites that are important for these swans' conservation. Tundra swans were captured at Kutcharo Lake, Hokkaido, in 2009–2012 and satellite-tracked. A new method called the "MATCHED (Migratory Analytical Time Change Easy Detection) method" was developed. Based on median, the spring migration began on 18 April and ended on 27 May. Autumn migration began on 9 September and ended on 2 November. The median duration of the spring and autumn migrations were 48 and 50 days, respectively. The mean duration at one stopover site was 5.5 days and 6.8 days for the spring and autumn migrations, respectively. The number of stopover sites was 3.0 and 2.5 for the spring and autumn migrations, respectively. The mean travel distances for the spring and autumn migrations were 6471 and 6331 km, respectively. Seven migration routes passing Sakhalin, the Amur River, and/or Kamchatka were identified. There were 15, 32, and eight wintering, stopover, and breeding sites, respectively. The migration routes and staging areas of tundra swans partially overlap with those of whooper swans, whose migration patterns have been previously documented. The migration patterns of these two swan species that winter in Japan confirm the importance of the Amur River, Udyl' Lake, Shchastya Bay, Aniva Bay, zaliv Chayvo Lake, zal Piltun Lake, zaliv Baykal Lake, Kolyma River, Buyunda River, Sen-kyuyel' Lake, and northern coastal areas of the Sea of Okhotsk.

Key words: *Cygnus columbianus*, the Eastern Palearctic flyway, migration pattern, stopover sites, tundra swans

INTRODUCTION

Tundra swans (*Cygnus columbianus*) breed in tundra regions near the North Pole, winter in temperate regions of the coastal areas of the Pacific and Atlantic Oceans, and spend as much as half of the year migrating between these regions (Nolet, 2006). Four tundra swan flyway populations have been identified: those corresponding to the WN (Western Nearctic), EN (Eastern Nearctic), WP (Western Palearctic), and EP (Eastern Palearctic) (Nolet, 2006).

Satellite tracking technology had been used to reveal the migration patterns and flyways of tundra swans. Nolet (2006) assessed the successful tracking of tundra swans in many studies, including Ely et al. (1997) (six tundra swans in the WN flyway), Petrie and Wilcox (2003) (19 individuals in the EN flyway), and Nowak et al. (1990) (three individuals in the WP flyway) and Beekman et al. (2002) (seven individuals in the WP flyway). Based on map interpretation of four flyways in Nolet (2006), the characteristics of these migration routes can be summarized as follows. The WN flyway is a route connecting Alaska and the western United States along the Rocky Mountains. The EN flyway passes between northern Canada and southeast United States through the Great Lakes. The WP flyway connects the Arctic Ocean at

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the northwest region of Russia and the United Kingdom through Scandinavian Peninsula. The EP flyway goes between southwest coast of Japan and the Arctic Ocean at the northeast region of Russia, passing through Hokkaido in Japan.

There have only been two reports on the EP flyway. The first satellite tracking of tundra swans for the EP flyway was reported by Higuchi et al. (1991), who tracked four tundra swans from Kutcharo Lake (45°1′N, 142°3′E) in Hokkaido, Japan. The second tracking was reported by Kamiya and Ozaki (2002), who tracked eight tundra swans from Nakaumi Lake (35°26′N, 133°17′E) in western Honshu, which is the most southerly lake that is regularly used by tundra swans that winter in Japan. However, these previous studies provided only limited information on migration, due to the limited number of successfully tracked swans (1–2 individuals in each study); they also lack information on autumn migration. Hence, the EP Flyway of tundra swans is considered the least known of the migratory paths. It is also important to understand the spring and autumn migration patterns of these birds.

The congeneric whooper swans (*Cygnus cygnus*) are expected to show similar characteristics on migration patterns to those of tundra swans. For example, Shimada et al. (2014) satellite-tracked whooper swans wintering in Japan to reveal migration routes, and described how the migration routes and staging areas of whooper swans overlapped at least partially with those of tundra swans. Recently, outbreaks of avian influenza have occurred in 2008, and infected swans were found in Japan (Newman et al., 2009). Understanding migration routes of tundra swans and whooper swans in East Asia more accurately can contribute to conservation of swans in East Asia as well as knowledge on potential transmission process of avian influenza viruses potentially carried by swans.

In the present study, 16 tundra swans were successfully satellite-tracked and analyzed to gain a better understanding of the migration and flyway of these birds. The objectives of this study were 1) to determine the migration pattern of the EP flyway of tundra swans; 2) to compare this pattern with that of whooper swans; and 3) to identify important stopover sites for these two swan species' conservation in East Asia. To achieve the above objectives, first, a new method, the "MATCHED (Migratory Analytical Time Change Easy Detection) method", was developed. Second, indices such as the duration of wintering, spring migration, breeding, autumn migration, staying period at stopover sites, number of stopover sites, and travel distance were calculated. Third, the migration routes for the spring and autumn migrations were identified. Fourth, wintering sites in Japan, stopover sites, and breeding sites in Russia were identified.

MATERIALS AND METHODS

Satellite tracking

In total, 27 Tundra Swans were captured during the winters of 2009 through 2012 (October to April) at Kutcharo Lake (45°07′28.560″ N, 142°20′45.743″ E) near the town of Hamatonbetsu, Hokkaido, Japan. There were 12 females and eight males. The sexes of seven individuals were unknown. All individuals were adults. The swans were captured using flat net traps or by hand. Captured swans were equipped with green neck collars and alpha-

numeric codes to which satellite transmitters (platform transmitter terminals; PTTs) were attached. The seven PTTs (PTT ID: 96824 to 96830) were programmed to transmit for 8 h and remain off for 23 h. The other PTTs (PTT ID: 93911 to 93917, 96816 to 96823, 78021, and 89040) were programmed to transmit for 9 h and remain off for 35 h. Three PTTs (PTT ID: 96817, 96819, 96826) were collected in field and reattached to other individuals. The PTTs used were solar-powered "SOLAR BIRDBORNE PTT" that weighed 12 g and were made by North Star Science and Technology LLC (King George, VA, USA). A PTT and neck collar weighs approximately 47 g and is approximately 0.9% of the swan's average body weight.

The PTT locations were estimated using the Argos System (Argos, 1996; CLS (Collecte Localisation Satellites), 2007). Data collected using the Argos System included the date, time (Greenwich Meridian Time; GMT), and longitude and latitude (WGS84 datum) with location accuracy. The location accuracy (location class, LC) was classified as 3, 2, 1, 0, A, B, and Z and was reported using the Argos System. Prior to statistical analysis, the data were filtered using The Douglas Argos-Filter Algorithm (Douglas et al., 2012; USGS Alaska Science Center, 2015). Data of a total of 16 individuals (PTT IDs and sex: 78021U, 89040M, 93913M, 93915F, 93917F, 96816U, 96819F, 96821M, 96822F, 96823U, 96824M, 96825M, 96826M, 96827F, 96828F, 96830M) were used in this study because these data were considered to be durable for migration pattern analysis. Six of these swans were females (F), seven were males (M), and the rest were unknown (U). The maximum tracking period was from 2009 to 2012.

Identification of dates to differentiate migration status

Tundra swans' migration can be classified according to migration status. These statuses included the wintering period, spring migration, breeding period, and autumn migration. Although variations in day length and weather conditions are important in determining the timing of their migration (Eileen, 2010), individual swans do not leave a wintering site on the same day due to various conditions, e.g., microhabitats and/or microclimates that each swan encounters in its habitat. To determine migration status, periods of these statuses must be individually determined. To our knowledge, however, there is no objective method to define 'a threshold date' for when an individual bird changes its status. For instance, Limiñana et al. (2007) used distance to estimate ending date of migration but did not address detecting all migration status. In this study, an effective method to determine threshold dates was developed and named the "MATCHED (Migratory Analytical Time Change Easy Detection) method". Following is a description of the MATCHED method.

The dataset was created as follows. After filtering through the Douglas Argos-Filter Algorithm, the bad location classes of LC 0, A, B, and Z were eliminated, and only good location classes, such as LC 3, 2, and 1, were retained for analysis. When there were several overlapping dates, a single date was selected by choosing better location classes. In situations when the same date had the same location class, the earlier record was selected. Geographic coordinates (x_i, y_i) in meters were calculated based on latitude and longitude in degree. The data in this study are presented as a spatiotemporal surface pattern $\{u(x_i, y_i, t_i)|i = 1, 2, \ldots, n\}$ with horizontal indexing space (x_i, y_i) (unit is m) in 2-D and t_i indicating the sampling time (the unit is the date). The distance between two points is the length of the path connecting them. In the plane, the distance between points (x_i, y_i) and (x_{i+1}, y_{i+1}) is given using the Pythagorean Theorem, $d_i = \sqrt{(x_{i+1} - x_i)^2 + (y_{i+1} - y_i)^2} \Big/ 1000$ to acquire the distance in km. In this study, d_i $(i = 1, 2, \ldots, n)$ was calculated individually. The distance of the first record of an individual was treated as $d_1 = 0$. Because data acquisition through the Argos System depended on variations in satellites, weather, etc., t_i could not be regularly sampled at an equal sampling spacing. As a result, there were numer-

ous missing dates in the dataset. Thus, the daily distance (v_i; unit is km/day) was derived using $v_i = \dfrac{d_i}{(t_{i+1} - t_i)}$; this distance was comparable for each subsequent record. The above data treatment was conducted using Microsoft Excel 2010. In the spatial analysis (ArcMap ver. 10 ®, ESRI Inc.), simple location indicators, such as Japan, ocean, or Russia, were compiled to represent single columns.

The R software version 3.1.3 (R Development Core Team, 2006) was used to analyze migration patterns as time-series data and to determine the threshold dates of the migration status. The "zoo" (Zeileis and Grothendieck, 2005; Zeileis et al., 2015) and "changepoint" (Killick et al., 2014; Killick and Eckley, 2014) of R packages were used. The change points in this study were defined as threshold dates between two consecutive migration statuses, e.g., wintering and spring migration. The migration status was defined as wintering, spring migration, breeding, or autumn migration. The migration status sequence is crucial for this analysis.

A time frame was created for each individual using "zoo". Each time frame was assigned to begin at the initiation of satellite tracking until the end date of satellite tracking for an individual. Because satellite tracking data often have missing data, the time series analysis needs to be able to be conducted with irregular time series data. Hence, the package "zoo" was suitable to analyze such data because it offer the advantage of unitizing irregular time series data, compared to capabilities of other time series packages in R.

The "changepoint" package can automatically identify threshold values. It is possible to identify a single change point or multiple change points. An ordered sequence of data, $z_{1:n} = (z_1, z_2, \ldots, z_n)$, is given. If a changepoint is said to occur within this set when a time is present, $\tau \in \{1, 2, \ldots, n-1\}$, two segments of $\{z_1, \ldots, z_\tau\}$ and $\{z_{\tau+1}, \ldots, z_n\}$ can be statistically differentiated. If a number of changepoints, m, together with their positions, $\tau_{1:m} = (\tau_1, \tau_2, \ldots, \tau_m)$, is given, each changepoint position is an integer between 1 and $n-1$ inclusive. It is defined that $\tau_0 = 0$ and $\tau_{m+1} = n$. The changepoints are assumed to be ordered as $\tau_i < \tau_j$ if $i < j$. Consequently, the m changepoints split the data into $m + 1$ segments with the ith segment containing the data $z_{(\tau_{i-1}+1:\tau_i)}$. Each segment is summarized using a set of parameters. To identify the optimal combinations, the daily distance, latitude, and longitude were respectively tested via

three scripts of changepoint package: "cpt.mean", "cpt.var", and "cpt.meanvar". The scripts "cpt.mean", "cpt.var", and "cpt.meanvar" can calculate threshold values based on changes in the mean, variance, and mean and variance, respectively. The combination of the "cpt.meanvar" method for latitude best fitted the data based on a visual comparison with migration patterns. Hence, this combination was used for all individuals. The number of changepoints was adjusted based on the length of the tracking period.

After the changepoints were identified using the above method, these threshold dates were plotted against backgrounds showing the latitude, longitude, and daily distance with the simple location indicators of Japan, the ocean, and Russia. The scales of latitude and longitude were adjusted with the scale of the daily distance so that the change patterns in these variables were visible in one graph. If the threshold dates were considered to be missed via automatic detection through "changepoint" analysis, these dates were manually identified based on plotted variable trends and geographic location, and manually added.

One example of the MATCHED method is given using PTT ID 96816 (Fig. 1). The MATCHED method was generally successful in identifying the migration status threshold dates for all of the swans. During wintering, the three latitude, longitude, and daily distance lines were generally flat and stable (28 December, 2009 to 29 April, 2010 in this example). In this case, 29 April is taken as the threshold date between wintering and spring migration. The starting date of wintering was unknown for this example. Flat and stable patterns for daily distance, longitude, and latitude suggest migration ends. The latitude and longitude in wintering sites were lowest which suggested that the swans remained in Japan which is located southwest compared to Russia. During spring migration, there was a clear step-like pattern indicating simultaneous increases in latitude and longitude (From 29 April 2010 to 3 July 2010). This pattern indicates that the swans moved northeast, i.e., from Japan to Russia. The daily distance showed several peaks. The number of peaks in daily distance and the number of steps according to longitude and latitude synchronized. These changes indicate stopovers, as the swans' geographic location should be the same during each stopover, but the daily distance should increase prior to reaching the stopovers. This daily distance over a short period of time is represented as a peak. After arriving at breeding or terminal sites, all
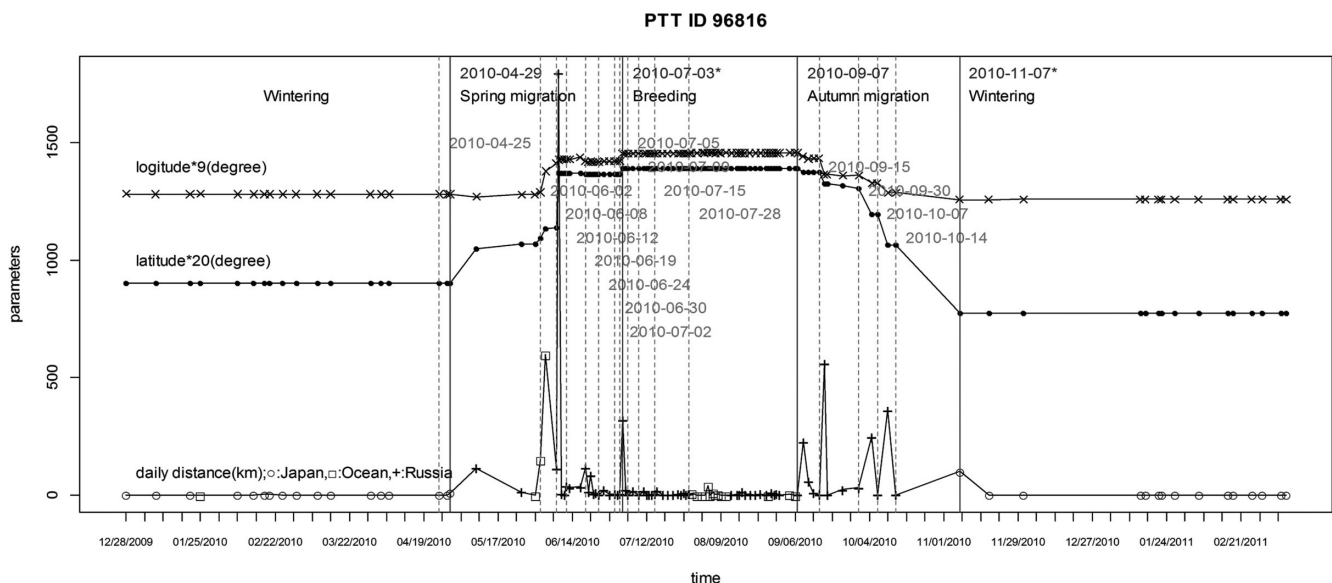

Fig. 1. Change points identified via the MATCHED method for an individual tundra swan (PTT ID 96816). 2010-07-23, the change point between spring migration and breeding, and 2010-11-07, the change point between autumn migration and wintering, were not automatically identified using a "changepoint" analysis.

daily distance, longitude, and latitude parameters became flat and stable, and the latitude and longitude reached their highest values during migration (3 July 2010 to 7 September 2010). The highest latitude and longitude values indicate that the swans reached their terminal sites in Far East Russia in the Arctic. The autumn migration shows a step-like shape with decreases in latitude and longitude (7 September 2010 to 7 November 2010). This result indicates that the swans moved southwest during autumn migration from the Arctic in Russia to their wintering sites in Japan.

The threshold dates delineating wintering, spring migration, breeding, and autumn migration were able to be identified using the MATCHED method. The stopovers were also generally identifiable using the MATCHED method; however, the stopover duration tended to be longer than the actual period. Thus, during the identified duration, the actual stopover periods were determined using geographical locations to confirm the proximity between consecutive points.

Calculation of migration indices

The migration indices, including the migration status start and end dates, the duration of the migration status, the duration and number of stopover sites, and the total travel distance between the wintering and breeding sites were individually calculated. The median and 25 and 75 percentiles of each index were calculated. The travel distance was calculated for individual birds using each bird's accumulated distance. The differences in the stopover duration between spring migration and autumn migration were tested using the Wilcoxon rank-sum test (Wilcoxon, 1945) via the exactRankTests (Torsten and Kurt, 2015) package, R software, version 3.1.3. The difference in the number of stopovers between the spring migration and autumn migration were analyzed using the same method.

Identification of spring migration routes and autumn migration routes

After applying the MATCHED method, threshold dates to identify spring migration and autumn migration were determined. Using these threshold dates, the dataset was filtered and classified to produce another dataset. This dataset included LC 3, 2, 1, 0, and A. The migration routes for the spring and autumn migrations were drawn separately using ArcMap ver. 10® (ESRI Inc.) with this dataset based on

Mercator projection.

Identification of wintering areas, stopover areas, and breeding areas

Using the MATCHED method, specific geographic location names, e.g., lakes, bays, rivers etc., were identified by manual map checking. For each individual, the mean centers were calculated
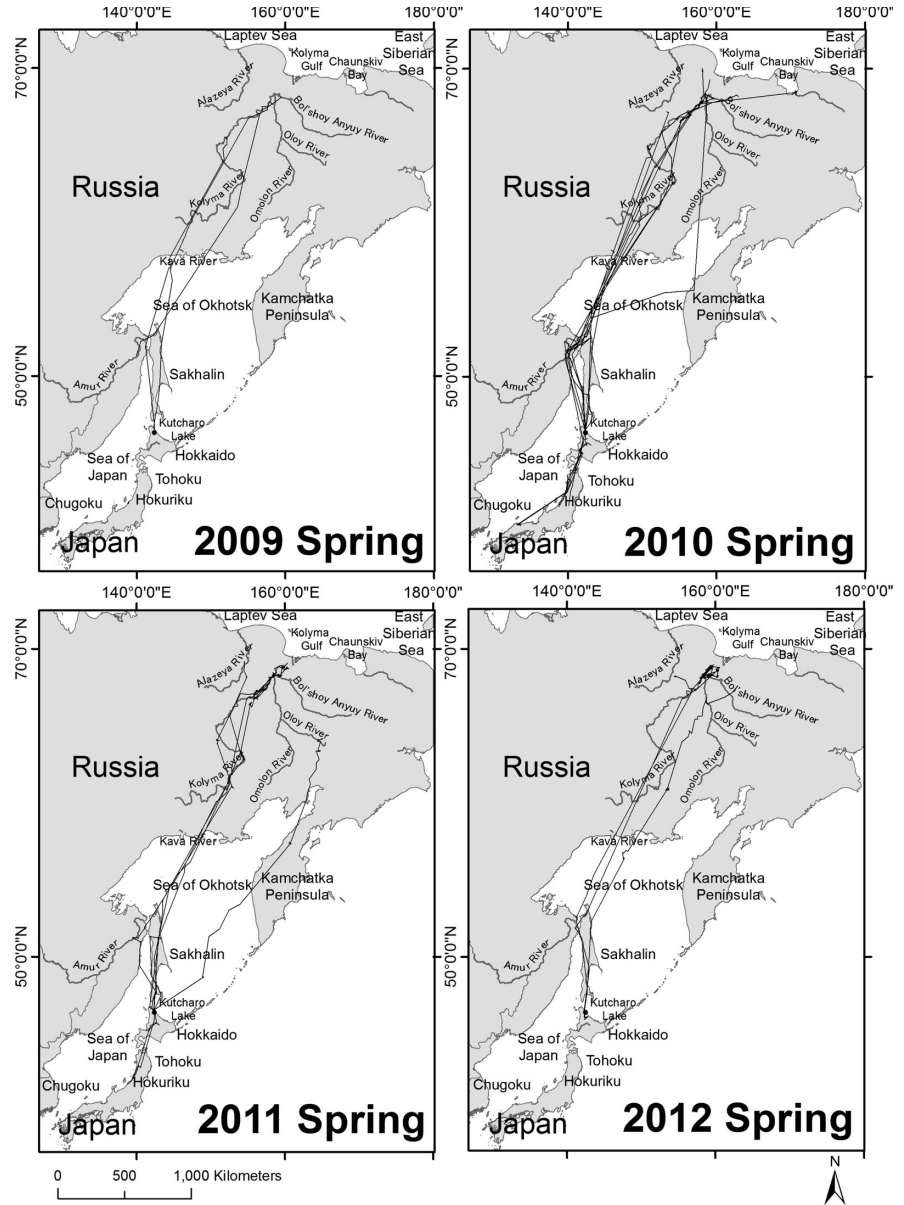

Fig. 2. Spring migration routes of tundra swans marked with satellite transmitters at one wintering site, Kutcharo Lake, Hamatonbetsu, Hokkaido, Japan, 2009–2012.

Table 1. Start date, end date, and duration of the wintering period, spring migration, breeding period, and autumn migration. The 1st quartile (Q1), the 3rd quartile (Q3) and median dates with sample sizes (n) are shown.

	Start date				End date				Duration (days)			
	Q1	~	Q3	Median	n	Q1	~	Q3	Median	n	Q1	~	Q3	Median	n
Wintering period	24-Oct	~	16-Nov	2-Nov	13	13-Mar	~	29-Apr	18-Apr	18	123	~	170	131	7
Spring migration	13-Mar	~	29-Apr	18-Apr	18	21-May	~	4-Jun	27-May	18	30	~	69	48	16
Breeding period	23-May	~	4-Jun	28-May	17	3-Sep	~	22-Sep	9-Sep	12	85	~	115	103	10
Autumn migration	3-Sep	~	22-Sep	9-Sep	12	24-Oct	~	16-Nov	2-Nov	13	42	~	63	50	10

using Spatial Statistics for ArcMap ver. 10® (ESRI Inc.) for the wintering areas, stopover areas, and breeding areas, respectively, to visualize various migration sites. The mean center was defined as a point constructed from the average x and y values for the input feature centroids. The stopover areas were categorized according to duration and location.

RESULTS

Calculation of indices of migrations

The start date, end date, and duration for the wintering period, spring migration, breeding period, and autumn migration were calculated (Table 1). There were several possible reasons for differences in the sample size of each event. First, the tracking periods differed for individual swans; second, some PTTs stopped functioning during migration; third, it was not always possible to successfully identify the threshold dates. Based on median values, wintering began on 2 November ($n = 13$) and ended on 18 April ($n = 18$); the spring migration began on 18 April ($n = 18$) and ended on 27 May ($n = 18$); breeding began on 28 May ($n = 17$) and ended on 9 September ($n = 12$); and the autumn migration began on 9 September ($n = 12$) and ended on 2 November ($n = 13$). The quartiles are shown in Table 1. The median durations for the wintering period, spring migration, breeding period, and autumn migration were 131 days, 48 days, 103 days, and 50 days, respectively. The start date and end date varied with the year.

The average duration at one stopover site for an individual was 5.5 ± 4.1 days ($n = 74$) and 6.8 ± 5.7 days ($n = 31$) for the spring and autumn migrations, respectively. There was no significant difference between the spring and autumn migrations according to stopover duration ($W = 1{,}156$, $P = 0.3226$, Wilcoxon rank-sum test). The number of stopover sites was 3.0 ± 2.8 ($n = 16$) and 2.5 ± 1.2 ($n = 9$) for the spring and autumn migrations, respectively. The number of stopover sites during spring migration for 96819F was 12.5, which was a considerably larger number than that for other individuals. There was no significant difference between the spring and autumn migrations regarding the number of stopovers ($W = 72.5$, $P = 0.9912$, Wilcoxon rank-sum test).

The mean travel distance for the spring and autumn migrations were 6,471 km (SD = 1,879 km, $n = 16$) and 6,331 km (SD = 604 km, $n = 12$), respectively.

Identification of spring and autumn migration routes

The spring and autumn migration routes are illustrated in Fig. 2 and Fig. 3, respectively. Seven routes were identified (Table 2, Fig. 4). For convenience, these routes were designated Routes A–G.

The most common flyway was Route A, which was used by seven swans for both seasons. Route A passed through Sakhalin. The second-most popular flyway was Route B (four swans). Route B passed through the mouth of the Amur River instead of Sakhalin. The third-most popular flyway was Route F, which passed through both the Amur River and Sakhalin once each. Only two tundra swans (78021U: Route E and 96816U: Route D) passed through the Kamchatka Peninsula during the spring migration; however, no individuals passed through this peninsula during the autumn migration (Figs. 2, 3, 4). Route C also experi-
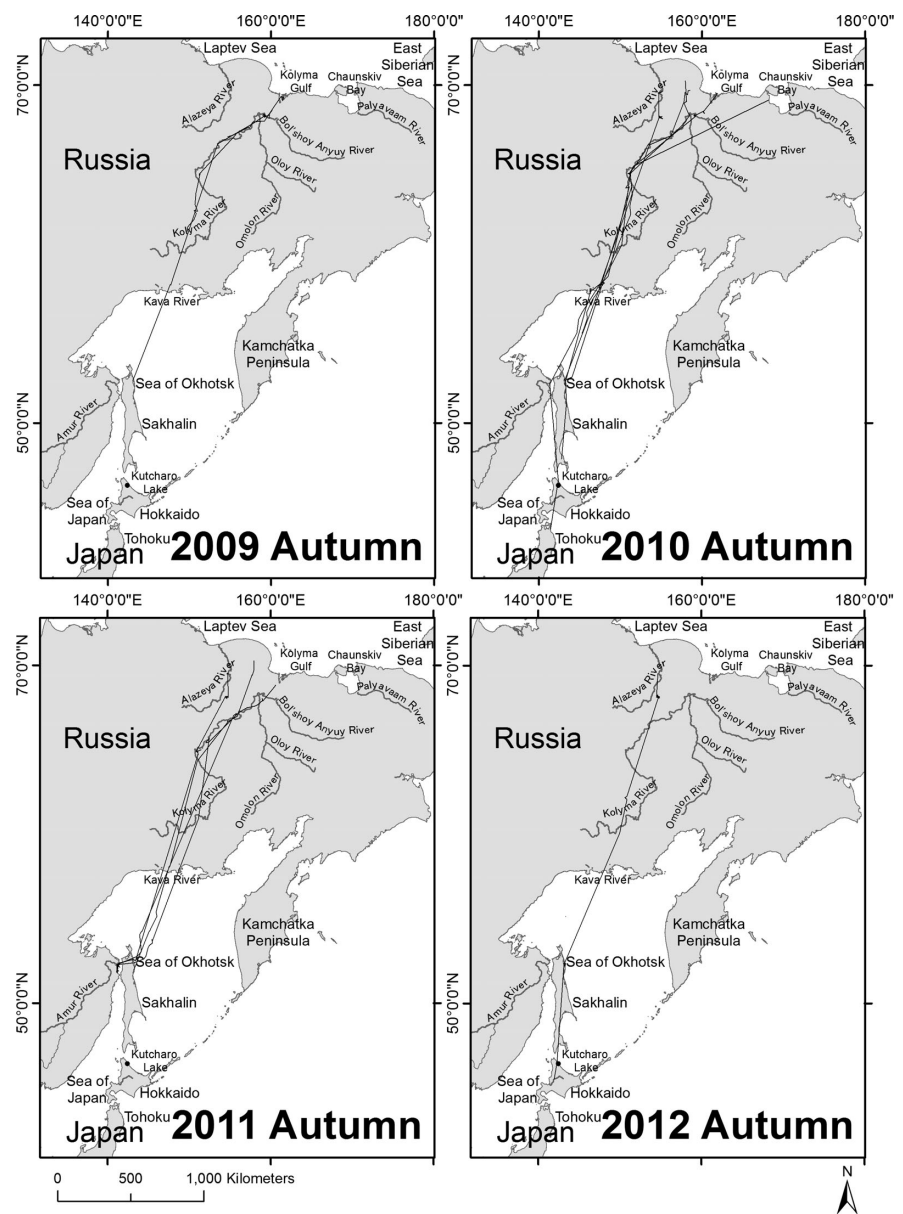

Fig. 3. Autumn migration routes of tundra swans marked with satellite transmitters at one wintering site, Kutcharo Lake, Hamatonbetsu, Hokkaido, Japan, 2009–2012.

Table 2. Seven identified migration routes for the EP (Eastern Palearctic) flyway of tundra swans.

Note:	Description	Spring	Autumn
A	Wintering sites in Japan-Hokkaido-Sakhalin-Sea of Okhotsk-(Kava River)-Kolyma River-Breeding sites in Russia	Used by 89040M, 93915F, 96822F 96824M, 96826M, 96827F	Used by 96822F, 96828F
B	Wintering sites in Japan-Hokkaido-Sea of Japan-Amur River-Sea of Okhotsk-(Kava River)-Kolyma River-Breeding sites in Russia	Used by 93913M, 96821M, 96822F, 96823U	Used by 96822F
C	Wintering sites in Japan-Hokkaido-Sakhalin-Sea of Japan-Amur River-Sea of Okhotsk-(Kava River)-Kolyma River-Breeding sites in Russia	Used by 96822F	
D	Wintering sites in Japan-Hokkaido-Sea of Japan-Amur Liman Ocean-Sakhalin-Sea of Okhotsk-Kamchatka-Kolyma River-Breeding sites in Russia	Used by 96816U	
E	Wintering sites in Japan-Hokkaido-Sea of Okhotsk-Kamchatka-Oloy River-Breeding sites in Russia	Used by 78021U	
F	Wintering sites in Japan-Hokkaido-Sea of Japan-Amur River-Sakhalin-Sea of Okhotsk-(Kava River)-Kolyma River-Breeding sites in Russia	Used by 93917F	Used by 89040M, 96819F, 96822F
G	Wintering sites in Japan-Hokkaido-Sakhalin-Sea of Japan-Amur River-Sakhalin-Sea of Okhotsk-(Kava River)-Kolyma River-Breeding sites in Russia	Used by 96819F, 96828F, 96830M	

Note: The Kava River was used only during autumn migration and not for spring migration. During spring migration, the tundra swans passed the coastline between the city of Okhotsk and the city of Magadan. The Kava River is in the middle.
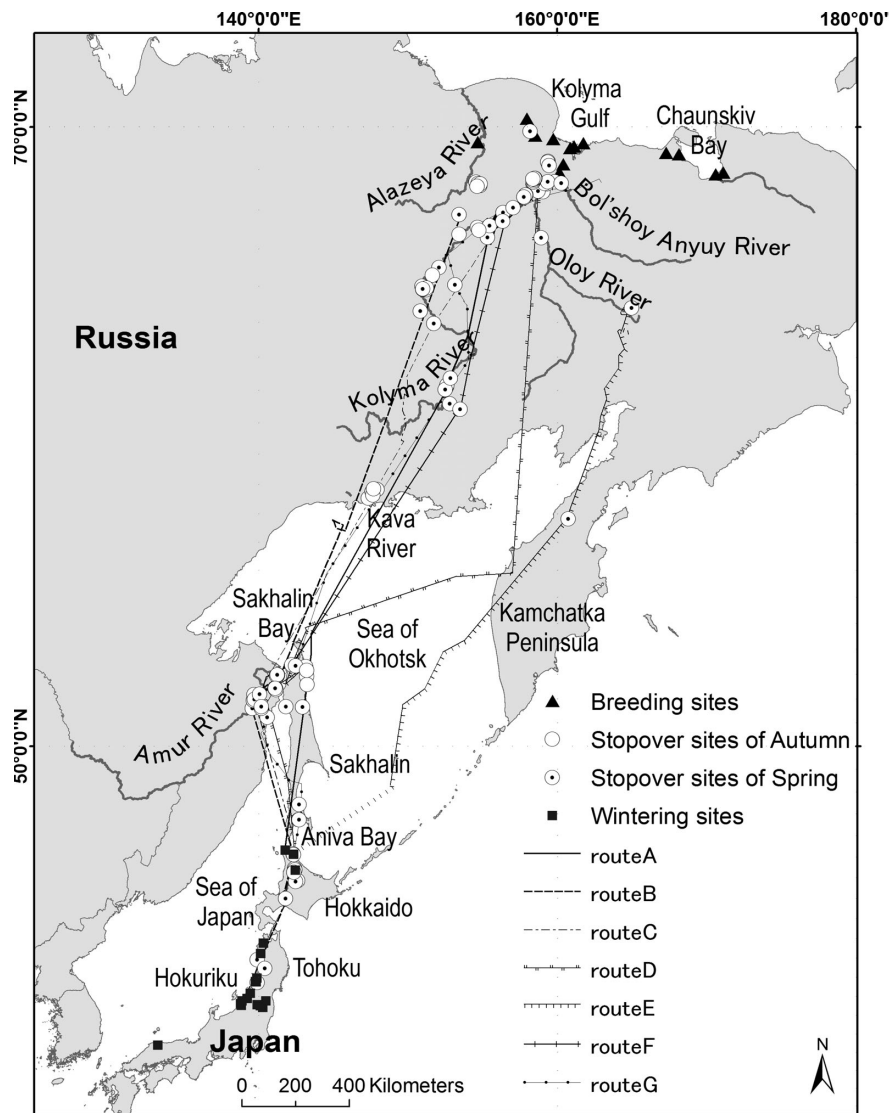

Fig. 4. Important migration sites and seven migration routes of tundra swans identified via satellite tracking.

enced sparse migration traffic. This route passed through Sakhalin and went to the Amur River through the Sea of Japan. Route G arrived at Sakhalin twice, on both sides of the Amur River, and was used only during the spring migration.

In the spring migration (Fig. 2), all of the swans departed from several wintering sites in Japan. Although most of the swans departed from Kutcharo Lake in the northeast region of Hokkaido, some departed from the main island of Japan (Honshu), such as from the Tohoku, Hokuriku, or Chugoku regions. There were three destinations for the first movement of tundra swans from wintering sites: Sakhalin (Routes A, C, G), the Amur River (Routes B, D, F), or Kamchatka Peninsula (Route E). The second decision diverged to create more complex routes (Table 2). If the swans went to Sakhalin, they passed through the Aniva Bay and/or Sakhalin Bay in southern Sakhalin. If the swans went to the Amur River, they arrived at the mouth of the river on the Eurasian continent. Four individuals did not go to Sakhalin and instead moved to the mouth of the Amur River through the Sea of Japan (Route B in Table 2). Some of the swans passed through the region close to the Kava River but never stopped in these areas during the spring migration. Most of the swans took the routes along the Kolyma River to reach the terminal sites in Far East Russia and the Arctic (six routes: Routes A, B, C, D, F, and G). One individual (1 route by 78021U) went to the

Kamchatka Peninsula and did not go to either Sakhalin or the mouth of the Amur River (1 route; Route E). One individual (96816U; Route D) migrated directly to the Amur Liman Ocean near the Tatar Strait (near the mouth of Amur River) through the Sea of Japan and went to the east coast of north Sakhalin but came back to the western coast of northern Sakhalin. After Sakhalin, this swan moved to the Kamchatka Peninsula and then to the wetland near the Kolyma Gulf. Destinations in Far East Russia depended on the individual. Popular destinations of the spring migration included locations downstream of the Kolyma and Bol'shoy Anyuy Rivers. One individual (96822F) preferred the Alazeya River. One individual (78021U) arrived at the Oloy River via the Kamchatka Peninsula. In the spring of 2010 and 2011, some Tundra Swans began to migrate from their southern wintering sites in Honshu. In 2010, one swan (96823U) began its spring migration from Nakaumi Lake in Shimane Prefecture, western Japan. This swan had a wintering period that began on 4 December 2009 and ended on 27 March 2010. According to differences in geographic locations, this swan was suspected to have had four wintering sites: Nakaumi Lake, the Mogami River, the Yoneshiro River, and the Iwaki River (W15, W6, W5, and W4, respectively, in Table 3). This swan began wintering at the Mogami River and remained from 3 December to 4 December 2009 but moved to Nakaumi Lake and remained there from 1 February to 10 February 2010. The swan then returned to the Mogami

Table 3. Geographic locations of wintering sites, stopover sites, and breeding sites used by tundra swans from 2009–2012.

No.	Prefecture/Province	City name/rayon[1]	Geographic location	Lat.	Long.
(A) Wintering sites					
W1	Hokkaido	Wakkanai	Koetoi River	141.791	45.329
W2	Hokkaido	Hamatonbetsu	Kutcharo Lake	142.346	45.128
W3	Hokkaido	Nayoro	Teshio River	142.453	44.378
W4	Aomori	Tsugaru	Iwaki River	140.32	40.777
W5	Akita	Noshiro	Yoneshiro River	140.146	40.239
W6	Yamagata	Sakata	Mogami River	139.892	38.97
W7	Fukushima	Koriyama	Abukuma River	140.391	37.598
W8	Fukushima	Inawashiro Lake	Inawashiro Lake	140.117	37.507
W9	Niigata	Niigata	Agano River	139.245	37.91
W10	Yamagata	Tsuruoka	Mogami River	139.821	38.785
W11	Niigata	Murakami	Arakawa River	139.454	38.169
W12	Niigata	Nagaoka	Shinano River	138.827	37.581
W13	Niigata	Niigata	Shinano River	138.896	37.772
W14	Niigata	Sanjo	Shinano River	139.918	37.571
W15	Shimane	Yasugi	Nakaumi Lake	133.255	35.396
(B) Stopover sites					
S1	Yamagata	Tsuruoka	Mogami River	139.903	38.732
S2	Akita	Daisen	Omono River	140.423	39.471
S3	Akita	Oga	Lagoon Hachiro[2]	139.907	39.92
S4	Hokkaido	Yuni	Ishikari River	141.817	42.997
S5	Hokkaido	Asahikawa	Ishikari River	142.494	43.817
S6	Hokkaido	Toma	Ishikari River	142.635	43.867
S7	Hokkaido	Nayoro	Teshio River	142.427	44.421
S8	Hokkaido	Shibetsu	Teshio River	142.377	44.266
S9	Hokkaido	Hamatonbetsu	Kutcharo Lake	142.335	45.126
S10	Sakhalin	Dolinskiy	Lebyazh'ye Lake	142.713	47.439
S11	Khabarovsk	Ul'chskiy	Sea of Japan	140.585	51.231
S12	Khabarovsk	Ul'chskiy	Amur River	139.988	51.635
S13	Sakhalin	Noglikskiy	Tym River	142.957	51.668
S14	Sakhalin	Aleksandrovsk-Sakhalinskiy	Sea of Japan	141.833	51.681
S15	Sakhalin	Anivskiy	Aniva Bay	141.713	46.742
S16	Khabarovsk	Ul'chskiy	Udyl' Lake	139.793	52.08
S17	Khabarovsk	Nikolaevskiy	Amur Liman Ocean[3]	141.128	52.426
S18	Sakhalin	Okhinskiy	Zaliv Chayvo Lake	143.262	52.6
S19	Khabarovsk	Nikolaevskiy	Shchastya Bay	141.255	52.969
S20	Sakhalin	Okhinskiy	Zal Piltun Lake	143.206	53.141
S21	Sakhalin	Okhinskiy	Zaliv Baykal Lake	142.358	53.37
S22	Koryak	Tigil'skiy	Palanskoye Lake	160.724	58.831
S23	Maga Buryatdan	Ol'skiy	Kava River	147.653	59.74
S24	Maga Buryatdan	Srednekanskiy	Buyunda River	152.809	62.609
S25	Maga Buryatdan	Srednekanskiy	Kolyma River	152.809	62.96
S26	Chukot	Bilibinskiy	Oloy River	164.965	65.419
S27	Sakha	Verkhnekolymskiy	Kolyma River	151.485	65.898
S28	Chukot	Bilibinskiy	Omolon River	158.915	67.304
S29	Sakha	Srednekanskiy	Kolyma River	156.158	67.917
S30	Sakha	Srednekolymskiy	Sen-kyuyel' Lake	154.711	68.646
S31	Sakha	Nizhnekolymskiy	Kolyma River	158.919	68.778
S32	Sakha	Nizhnekolymskiy	Bolshoye Morskoye Lake	158.171	69.903
(C) Breeding sites					
B1	NA	NA	East Siberian Sea	161.112	69.546
B2	Sakha	Nizhnekolymskiy	Bolshoye Morskoye Lake	158.246	69.991
B3	Sakha	Nizhnekolymskiy	Alazeya River	154.673	69.648
B4	Sakha	Nizhnekolymskiy	Kolyma River	160.583	69.381
B5	Sakha	Srednekolymskiy	Kolyma River	156.103	67.901
B6	Chukot	Bilibinskiy	Proliv Malyy Chaunskiy Bay	167.286	69.394
B7	Chukot	Chaunskiy	Proliv Malyy Chaunskiy Bay	168.136	69.361
B8	Chukot	Chaunskiy	Palayavaam River	170.867	68.904

[1] The term "rayon" in Russia is a type of administrative unit used in several post-Soviet states and is both a subnational entity and a division within a city. This term is commonly translated in English as a "district". [2] Lagoon Hachiro or the surrounding ocean at the Oga Peninsula was used. [3] The bay name could not be identified. The bay is near the Tatar Strait in Amur Liman.

River on 22 February 2010. It moved to the Yoneshiro River and remained there from 25 February to 5 March 2010 and moved to the Iwaki River and remained there from 12 March to 18 March 2010. Finally, the swan moved to Kutcharo Lake and remained there from 5 April to 20 April 2010 and then began moving toward Russia. It was uncertain whether these locations were stopover sites or wintering sites. There were two potential threshold dates based on the MATCHED method, 10 February or 27 March, as potential starting dates for spring migration.

During the autumn migration (Fig. 3), the swans departed from different breeding sites: downstream of the Alazeya River, downstream of the Kolyma River, downstream of the Bol'shoy Anyuy River, and the Chaunskiy Bay, which was located close to the East Siberian Sea. Similar to the spring migration, all of the swans moved along the Kolyma River

and reached the Kava River. The swans stopped at the Kava River only during autumn migration. From the Kava River, they traveled to only two destinations: Sakhalin (Route A, F) or the Amur River (Route B). They traveled over the Sea of Okhotsk and arrived at the mouth of the Amur River or northern Sakhalin. The most common flyway for autumn migration was Route F, for which the swans arrived at Sakhalin via the Sea of Okhotsk, moved to the Amur River, and finally returned to Hokkaido through the Sea of Japan (three swans; Route F, Table 2). Two swans (96822F in 2012 and 96828F; Route A) first visited Sakhalin followed by Hokkaido. One individual (96822F in 2010; Route B) did not visit Sakhalin but went to the mouth of the Amur River and came back to Hokkaido. This swan continued travelling to the Aomori Prefecture in the Tohoku region (Fig. 3).

Table 4.   Different use of stopovers during the spring and autumn migrations of Tundra Swans.

No.[1]	Geographic location	Individuals (PTT ID)	Spring migration	Autumn migration
S1	Mogami River	96828F	Used	
S2	Omono River	96828F	Used	
S3	Lagoon Hachiro	93913M	Used	
S4	Ishikari River	96828F	Used	
S5	Ishikari River	96828F	Used	
S6	Ishikari River	96822F	Used	
S7	Teshio River	96822F, 96826M	Used	
S8	Teshio River	96828F	Used	
S9	Kutcharo Lake	96822F, 96823U	Used by 96823U	Used by 96822F
S10	Lebyazh'ye Lake	96827F	Used	
S11	Sea of Japan	96819F	Used	
S12	Amur River	96819F, 96828F	Used	
S13	Tym River	96827F	Used	
S14	Sea of Japan	96828F	Used	
S15	Aniva Bay	96819F, 96828F	Used	
S16	Udyl' Lake	96821M, 96822F, 96823U, 96825M	Used	
S17	Amur Liman Ocean	96819F, 96822F, 96830M	Used by 96819F, 96822F	Used by 96819F, 96830M
S18	Zaliv Chayvo Lake	96827F		Used
S19	Shchastya Bay	89040M, 96819F		Used
S20	Zal Piltun Lake	96816U, 96826M, 96828F	Used by 96826M	Used by 96816U, 96828F
S21	Zaliv Baykal Lake	96816U, 96825M	Used	
S22	Palanskoye Lake	78021U	Used	
S23	Kava River	93913M, 96816U, 96822F, 96825M, 96827F		Used
S24	Buyunda River	96819F	Used	
S25	Kolyma River	89040M, 96822F, 96826M, 96827F	Used	
S26	Oloy River	78021U	Used	
S27	Kolyma River	93915F, 93917F, 96816U, 96819F, 96822F, 96823U, 96825M, 96827F, 96828F, 96830M	Used by 93915F, 96819F, 96823U, 96825M, 96830M	Used by 93917F, 96816U, 96822F, 96827F, 96828F
S28	Omolon River	96826M	Used	
S29	Kolyma River	89040M, 93913M, 93917F, 96816U, 96819F, 96822F, 96824M, 96825M, 96827F, 96828F	Used by 89040M, 93917F, 96816U, 96819F, 96822F, 96824M, 96825M, 96827F, 96828F	Used by 93913M, 96827F
S30	Sen-kyuyel' Lake	96822F	Used by 96822F	Used by 96822F
S31	Kolyma River	89040M, 93913M, 96816U, 96819F, 96827F	Used by 96816U, 96819F, 96827F	Used by 89040M, 93913M, 96816U, 96827F
S32	Bolshoye Morskoye Lake	96827F	Used	

   [1] "No." corresponds to the "No." in Table 3.

Identification of wintering areas, stopover areas, and breeding areas

A map of the identified wintering, stopover, and breeding areas with the seven routes is given in Fig. 4. Detailed geographic locations with latitude and longitude are explained in Table 3. There were 15 wintering sites, 32 stopover sites, and eight breeding sites in total (Table 3). All areas were related to water (rivers, lakes, lagoons, bays, and oceans). Kutcharo Lake, the Teshio River, and the Mogami River were used as both wintering sites and stopover sites. The Nakaumi Lake in the Shimane Prefecture (W15) represented the westernmost and southernmost wintering site in Japan. During stopover site stays, the Tundra Swans often preferred large lakes or long rivers that cross several cities in Japan or districts in Russia; the Ishikari River and Kolyma River are examples. One swan (78021U) used a stopover called Palanskoye Lake in the Kamchatka Peninsula. In Sakhalin, the southern region around Aniva Bay (S15), the middle region (S13, S14), and the northern region around Sakhalin Bay (S10, S18, S20, S21) were used as stopovers.

Stopover site differences were examined according to seasons (Table 4). Of the 32 stopover sites, 29 were used for spring migration and 10 were used for autumn migration. Seven stopover sites were used in both spring and autumn migrations: Kutcharo Lake, Amur Liman Ocean, zal Piltun Lake, the Kolyma River (S27, S29, and S31 in different counties), and Sen-kyuyel' Lake. Three stopovers were used during only autumn migration: zaliv Chayvo Lake, Shchastya Bay, and the Kava River.

DISCUSSION

Migration and EP flyway of tundra swans

Although there was no significant difference ($P < 0.05$) between the spring migration and autumn migration, the tundra swans remained in one stopover location for a longer period and in a more limited number of stopover sites during the autumn migration. The short travel distance during the autumn migration indicates that tundra swans take a short-cut during autumn migration to fly more efficiently than during the spring migration.

Previous studies (Higuchi et al., 1991; Kamiya and Ozaki, 2002) have used satellite tracking to show routes taken by tundra swans wintering in Japan. Four tundra swans tracked from Kutcharo Lake, Hokkaido (Higuchi et al., 1991) moved north over Sakhalin and stopped in northern Sakhalin or near the mouth of the Amur River. One swan was tracked to the mouth of the Kolyma River. Eight tundra swans were tracked from Lake Nakaumi in the Tottori and Shimane Prefectures in southwestern Japan and followed at least two spring migration routes (Kamiya and Ozaki, 2002): one route along the northern coast of the Japanese islands and the other directly across the Sea of Japan; although none of swans were successfully tracked to the breeding ground in the Russian Tundra. Our results are in accordance with those of previous studies; however, our study can add new information on migration routes to them with many more samples. In our study, seven tundra swan migration routes were identified for the EP flyway. One flyway directly crossing the Sea of Japan from Lake Nakaumi found by Kamiya and Ozaki (2002) was not detected in our study; however, all other flyways found by Higuchi et al.

(1991) and Kamiya and Ozaki (2002) were confirmed. The routes identified by Higuchi et al. (1991) are considered to be equivalent to Routes A, B and likely Route E as well. Hence, there are at least 8 flyways in the EP flyway for Tundra Swans wintering in Japan: Seven routes (Routes A–G in Table 2) detected in this study, and one more flyway which directly crosses the Sea of Japan reported by Kamiya and Ozaki (2002) in previous study.

This study identified 15 wintering sites, 32 stopover sites, and eight breeding sites (Table 3). Although all stopover sites are important, it may be most critical to conserve the following stopover sites: 1) Kutcharo Lake, the Amur Liman Ocean, zal Piltun Lake, the Kolyma River and Sen-kyuyel' Lake (representing frequently used stopover sites for both spring and autumn migrations), as well as 2) zaliv Chayvo Lake, Shchastya Bay, and the Kava River stopover sites (used during only autumn migration).

Comparison with whooper swans

Shimada et al. (2014) reported on the duration at stopover sites and the number of stopover sites for whooper swans wintering in Japan. According to Shimada et al. (2014), the duration at stopover sites for whooper swans captured at Lake Kussharo in Hokkaido was 13.4 ± 8.6 days and 17.1 ± 12.1 days for the spring and autumn migrations, respectively. The number of stopover sites for Whooper Swans captured at Lake Kussharo in Hokkaido was 1.9 ± 0.8 and 1.5 ± 0.5 for the spring and autumn migrations, respectively (Shimada et al., 2014). The definition of the start and arrival at a site differs between Shimada et al. (2014) and the current study; however, our data suggest that the stopover duration is shorter and that the number of stopover sites is a little greater for Tundra Swans.

Whooper swans and tundra swans are considered to have differing destinations in Russia. The stopovers of tundra swans along the Kolyma River appear to be terminal sites for whooper swans. Tundra swans migrate farther north than whooper swans. This finding is in agreement with findings by Higuchi et al. (1991). Tundra swans' terminal or breeding sites in Russia include the East Siberian Sea, Bolshoye Morskoye Lake, the Alazeya River, the Kolyma River, Proliv Malyy Chaunskiy Bay, and the Palayavaam River (Table 3). These sites are located close to the coastline of the northeast Far East Russia of the Arctic. These areas include the arctic tundra, which contains a great number of lakes and marshes of various sizes (Higuchi et al., 1991). The Indigirka River provides many important stopover sites and terminal sites for whooper swans; however, this river is not important for tundra swans. There appear to be few shared habitats between whooper and tundra swans wintering in Japan.

Conservation of swans in East Asia

In agreement with Shimada et al. (2014), the migration routes and staging areas of whooper and tundra swans are considered to partially overlap. Important wintering locations for these swan species include the mouth of Amur River, Udyl' Lake (mouth of the Amur River), Shchastya Bay (mouth of the Amur River), Aniva Bay (south Sakhalin), zaliv Chayvo Lake (north Sakhalin), zal Piltun Lake (north Sakhalin), zaliv Baykal Lake (north Sakhalin), the Kolyma

River, the Buyunda River (near the southern Kolyma River), Sen-kyuyel' Lake (the Kolyma River), and the northern coastal areas of the Sea of Okhotsk. Various conservation issues for these areas include habitat destruction and deterioration, collisions with wind turbines, chemical and radioactive pollutants, and hunting pressure. It is difficult to determine the impacts of these factors in each of the areas; however, these should be clarified in efforts to conserve the swans. Though the swans are not currently endangered, the above conservation issues are becoming increasingly serious and may cause drastic declines in swan populations in the near future.

Recent outbreaks of avian influenza through migratory birds are also of concern (Olsen et al., 2006; Newman et al., 2009). In Japan, whooper swans were infected with H5N1 avian influenza in northern Japan in 2008, and tundra swans were infected with H5N8 avian influenza in Nakaumi Lake in Shimane Prefecture in 2014. The swans winter with migratory ducks that can transmit such viruses. The spring and autumn migration routes described in this study will provide useful information in determining potential transmission patterns and the spread of avian influenza viruses by these waterfowl that winter in Japan.

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