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*Original paper*

# Migration routes and important stopover sites of endangered oriental white storks (*Ciconia boyciana*) as revealed by satellite tracking

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***Abstract:*** From 1998 through 2000, we tracked the autumnal migrations of 13 oriental white storks (*Ciconia boyciana*) by satellite in order to identify their important stopover sites. The storks were successfully tracked and provided data on partial ($n = 4$) or complete ($n = 9$) autumnal migration between the Russian Far East breeding sites and the wintering sites in southeastern China. Twenty-seven stopover sites were identified, the most important of which were in Tonghe Peat Moor (46.095°N, 128.942°E), Momoge Nature Reserve (45.945°N, 123.939°E), and Jiantuozhi Gley Mire (39.221°N, 118.672°E). The connectedness between each stopover site and its surrounding stay sites was also evaluated; the results suggested that the stopover sites situated on the seashores of Liaodong Bay, Bohai Bay, and Laizhou Bay in eastern China are less connected than the others. We concluded that, among the sites studied, Jiantuozhi Gley Mire on the northern shore of Bohai Bay should have a higher priority for protection for two reasons: it is used by many storks, in common, for relatively long periods; and it is at higher risk of being isolated from the migration route network.

**key words:** oriental white stork, satellite tracking, migration route, stopover site

## Introduction

The identification of migration routes and stay sites (including breeding and wintering sites, as well as stopover sites) is crucial to the effective conservation of any migratory bird (Berthold and Terrill, 1991). For more than a century, the banding method has been used to obtain data for hypothesizing about migration routes, range size, and nesting site fidelity of many migratory bird species. However, the data obtained by this traditional method have seldom attained the spatio-temporal resolution necessary to reveal exact migration routes and stopover sites, due to difficulties in resighting or recapturing the banded birds. Recent advances in the technology of satellite tracking have allowed researchers to continuously track the movements of individual birds over a broad spatial scale without conducting extensive field observations after the birds have been equipped with satellite transmitters. The applications of satellite tracking to bird migration studies have enabled considerable progress to be made with regard to elucidating the migration routes and stay sites of various migratory bird species, with important implications for conservation (Higuchi *et al*., 1996, 1998; Osborne *et al*., 1997; Petrie and Rogers, 1997; Fuller *et al*., 1998; Lorensten *et al*., 1998; Ueta *et al*., 1998, 2000, 2002; Pütz *et al*., 2000; Berthold *et al*., 2001; Kanai *et al*., 2002).

The oriental white stork (*Ciconia boyciana*) is one of the migratory wetland-obligate bird species whose numbers continue to decline. The current population of this species is estimated to be approximately 2500, and its IUCN Red List status is endangered (BirdLife International, 2001). Remnant populations breed primarily in the Russian Far East on the Amur, Ussuri, Zeya, Bikin, Urmi, and Bureya River floodplains, and in northeastern China around Lake Khanka (Smirenski, 1991). They migrate south in groups to overwinter, mainly, in southeastern China, around lakes situated along the middle reaches of the Yangtze River (Wang, 1991). The conservation of the species is closely tied to the protection of their wetland habitats, including breeding and wintering sites as well as stopover sites. Without proper conservation measures, stopover sites may become weak links in the chain of migration and, if broken, will probably signal the end of the wild populations that rely on them (Higuchi, 1991).

The migrations of oriental white storks pass through some of the most populated areas in the world, including the eastern plains of China, an area that has been experiencing rapid economic and population growth in recent years (United Nation, 2001; World Bank, 2002). The rapid developments linked to this growth have brought about the loss and degradation of wetland habitats for many wetland-obligate bird species (Asia-Pacific Migratory Waterbird Conservation Committee, 2001). The Russian and Chinese governments have been taking action with regard to bird and wetland conservation by establishing nature reserves, but these efforts have been directed mainly toward breeding and wintering sites. The lack of detailed background knowledge on the storks' migrations has constituted an obstacle to finding an adequate compromise between habitat protection and economic development in the regions along their migration routes.

We succeeded in the satellite tracking of the movements of oriental white storks on their autumnal migrations from 1998 through 2000. The preliminary results on their migration routes were reported using the dataset obtained in 1998 and 1999 (Higuchi *et al*., 2000). Here we compile all the data obtained during our three-year study to show the exact migration routes and the geographic locations of stopover sites. Furthermore, we identify important stopover sites, based on the number of visiting birds and the length of their stay. In addition, we evaluate the connectedness between each important stopover site and its neighboring stay sites (breeding, wintering, and stopover) in order to discuss the geographic condition of each important stopover site.

## Materials and methods

Satellite tracking data

From late June to mid-July each year from 1998 through 2000, 13 young oriental white storks, very close to fledgling age, were captured on the floodplains of the Amur and Ussuri Rivers in the Russian Far East (46–51°N, 127–136°E). To allow tracking *via* satellite, the storks were fitted with satellite transmitters (platform transmitter terminals, PTTs) as backpacks with Teflon-treated ribbons, according to the method described by Nagendran *et al*. (1994), and then released immediately. The weight of the backpack unit constituted less than

2% of the bird's body weight at the time of attachment. The details of the capture and PTT deployment methods were described by Higuchi *et al*. (2000).

The locations of the storks equipped with PTTs were determined by Argos and were reported as latitude and longitude pairs, based on the geodetic datum WGS84. The measurement time of each location point was given as GMT. An accuracy index (location class, LC) was also assigned to each estimated location point, based on the level of positional accuracy and the number of transmissions used for the location determination. Since June 1994, LC has been categorized into six classes (LC 3, 2, 1, 0, A, and B) using new algorithms (Argos, 1996). The level of location accuracy for each LC is defined by Argos as the standard deviation of the positional error in both longitudinal and latitudinal axes as follows: < 150 m for LC 3; between 150 and 350 m for LC 2; between 350 and 1000 m for LC 1; and > 1000 m for LC 0. Location accuracies for LCs A and B are not stated by Argos.

A total of 3542 location points were obtained for the movements of the 13 storks until the PTTs stopped functioning (Table 1). Of these, the points of LCs 3, 2, and 1 (approximately 40%) were used in our analyses. The points of LCs 0, A, and B were referred to on the map only for visual inspection of migration routes when higher accuracy data points were unavailable for three or more days.

Calculation of travel distance, speed and direction

The travel distance and direction between two location points were calculated as the geodesic distance and azimuth between the two points on the ellipsoid, based on the geodetic datum WGS84, using Vincenty's inverse formulae (Vincenty, 1975). The intervening time interval between two points was calculated as the difference between the measurement times at the points. The travel speed between two points was calculated by dividing the travel distance by the intervening time interval.

To determine the migration state of the stork at each location point, we calculated two kinds of travel speeds in km/d: (1) the speed of approach to the point of interest from a precedent point; and (2) the speed of departure from the point of interest to a subsequent point. From among all precedent (or subsequent) points with time intervals of longer than 24 h from the point of interest, the point nearest in time to the point of interest was selected as the precedent (or subsequent) point used in the calculations. Likewise, two kinds of travel directions (approach and departure) were calculated for each location point using the same point pair used in the calculation of travel speed. Then, the difference between the two travel directions was calculated as the deflection angle of the consecutive travel directions at each location point.

Determination of migration state

The migration state of the stork at each location point was determined, based on the following decision rule (1), assuming that different migration states can be characterized by different patterns of consecutive travel speeds:

$$\left.\begin{array}{l} \textit{if (approach speed} \le T\textit{) and (departure speed} \le T\textit{), then "stay";} \\ \textit{if (approach speed} > T\textit{) and (departure speed} > T\textit{), then "travel";} \\ \textit{if (approach speed} > T\textit{) and (departure speed} \le T\textit{), then "arrival";} \\ \textit{if (approach speed} \le T\textit{) and (departure speed} > T\textit{), then "departure",} \end{array}\right\} \quad (1)$$

Table 1. Summary of satellite tracking data for the 13 young oriental white storks tracked from their natal sites in the Russian Far East.

| PTT-ID | Capture (natal) site | | Tracking period (MM/DD/YY in GMT) | No. of location points for each LC | | | | | The last location of the storks tracked partially |
|---|---|---|---|---|---|---|---|---|---|
| | Latitude | Longitude | | 3 | 2 | 1 | Others | Total | |
| 09086 [a] | 49.865° N | 127.656° E | 07/10/98 - 02/07/99 | 104 | 89 | 88 | 144 | 425 | |
| 20846 [c] | 50.859° N | 129.083° E | 07/08/98 - 12/23/98 | 16 | 42 | 145 | 334 | 537 | A salt swamp in the Laizhou Bay seashore. |
| 20853 [a] | 49.200° N | 129.931° E | 07/03/98 - 01/21/99 | 31 | 86 | 265 | 545 | 927 | |
| 20818 [c] | 48.689° N | 134.602° E | 08/01/99 - 11/27/99 | 15 | 32 | 25 | 90 | 162 | A wetland site in the northern Bohai Bay seashore. |
| 20820 [a] | 48.640° N | 134.370° E | 08/01/99 - 04/05/00 | 6 | 14 | 22 | 70 | 112 | |
| 20821 [a] | 49.429° N | 129.674° E | 08/02/99 - 07/23/00 | 24 | 47 | 71 | 174 | 316 | |
| 20823 [a] | 49.289° N | 135.560° E | 08/09/99 - 07/07/00 | 8 | 16 | 28 | 108 | 160 | |
| 19033 [a] | 49.384° N | 129.835° E | 06/28/00 - 09/06/01 | 1 | 12 | 19 | 105 | 137 | |
| 19043 [c] | 49.371° N | 129.589° E | 06/26/00 - 10/31/00 | 0 | 8 | 28 | 102 | 138 | A wetland site in the northern Bohai Bay seashore. |
| 19361 [b] | 49.444° N | 130.080° E | 07/26/00 - 04/11/01 | 4 | 13 | 36 | 163 | 216 | |
| 19460 [a] | 48.836° N | 133.037° E | 06/29/00 - 04/01/01 | 2 | 7 | 44 | 70 | 123 | |
| 19628 [c] | 49.426° N | 129.661° E | 06/25/00 - 10/16/00 | 1 | 9 | 31 | 52 | 93 | The Shuangtaizi River delta facing Liaodong Bay. |
| 19640 [a] | 46.479° N | 133.642° E | 07/14/00 - 11/14/00 | 2 | 10 | 31 | 153 | 196 | |

[a] Storks that reached their well-known wintering sites on the Yangtze River floodplain in southeastern China.

[b] Stork that unexpectedly wintered at the region along the river that flows 100 km southwest of Beijing.

[c] Storks from which signals stopped at various sites in China before their arrivals at wintering sites were confirmed.

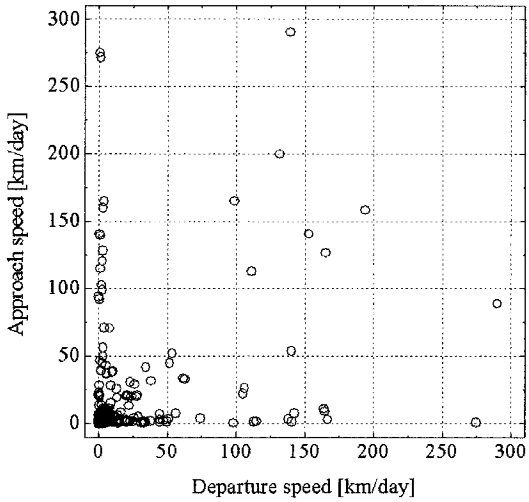


Fig. 1 Two-dimensional feature space defined by approach speed and departure speed.

where $T$ is the threshold travel speed in km/d; "stay" is the state of a bird being stationary within a specific range; "travel" is the state of a bird moving from one site to another; "arrival" is the state shifting from "travel" to "stay"; and "departure" is the state shifting from "stay" to "travel".

To select an appropriate threshold $T$, we clustered the location points with similar characteristics in approach speed and departure speed using the ISODATA algorithm (Ball and Hall, 1965). The ISODATA algorithm was implemented by taking the following steps:

(1) Map all location points into the two-dimensional feature space defined by approach speed and departure speed (Fig. 1) and specify the positions of 100 initial cluster centers to be uniformly spaced over the range between 0 and 300 km/d on the feature space.
(2) For the first iteration, assign each candidate point to the closest cluster by computing the Euclidean distance between the candidate point and each initial cluster center. Then, merge any clusters containing less than four points into the closest cluster.
(3) Recalculate all cluster centers.
(4) For the second iteration, reassign each candidate point to the closest cluster by computing the Euclidean distance between the candidate point and each cluster center. Then, merge any clusters containing less than four points into the closest cluster.
(5) Recalculate all cluster centers.
(6) Repeat procedures (4) and (5) until all cluster centers become unchanged between iterations.

After the completion of clustering, a label of "stay" or "travel" was tentatively assigned to the resultant clusters on the basis of the following assumptions: if a cluster consisted of "stay" points, its center would occur at a relatively low-speed part of the feature space and the deflection angles of the cluster points would vary widely, due to inconsistent movements in consecutive travel directions; and second, if a cluster consisted of "travel" points, its center would occur at a relatively high-speed part of the feature space and the variation in the deflection angles would be small due to the directional movements. Neither the "stay" nor the "travel" labels were assigned to clusters with no distinguishable properties. The appropriate threshold $T$ was then defined by averaging the maximum travel speed of "stay" cluster points and the minimum travel speed of "travel" cluster points.

### Identification of important stopover sites

First we determined the geographic location and extent of stay sites by specifying the area attainable by a bird moving at $T$ km/d for one day from the location points labeled as "stay", "arrival", and "departure." The geographic coordinates (latitude and longitude) of the centroid of each distinct stay site were calculated as the representative coordinates of each stay site. A sequential number was assigned to each site in latitudinal order for site identification (site-ID).

Next, each distinct stay site was categorized into one of three types (*i.e.*, breeding, wintering, or stopover). The stay sites containing location points at which storks were captured were regarded as breeding (or natal) sites; stay sites at which storks remained during the winter or until the start of the northward migration were regarded as wintering sites; and the remaining stay sites were considered stopover sites.

The relative importance of each stopover site was evaluated based on both the number of visiting birds and the length of stay. The length of the stay period of a stork at a site was defined as the intervening time interval between "arrival" and "departure" points recorded within the site. If the identification of "arrival" and/or "departure" points within the site failed, the length of stay at the site was left unknown.

### Evaluation of site connectedness

To discuss the geographic condition of each important stopover site, we evaluated "site connectedness". Site connectedness at the site of interest was defined as the number of neighboring stay sites located within the accessible distance $D$ from the site. That is, site connectedness is a measure relating to the accessibility, for the migrating storks, of the site to its neighboring stay sites. The sites with lower connectedness were considered to be at higher risk of being isolated from the migration route network.

The accessible distance $D$ was determined as the farthest distance that most of the tracked storks could travel without making stopovers en route. It was calculated using the equation: $D = \bar{v} \times t$, where $\bar{v}$ is the mean travel speed (in km/d) exhibited by the storks traveling between stay sites; and $t$ is the maximum length of time (in days) during which the storks traveled without making stopovers.

## Results

### Migration routes

Of the 13 oriental white storks equipped with PTTs, nine were tracked over their entire autumnal migrations to wintering sites, and four were tracked during part of their autumnal migrations (Fig. 2). Of the nine fully tracked storks, eight reached a wintering ground on the floodplain along the middle Yangtze River in southeastern China; the remaining one stork wintered 100 km southwest of Beijing, China. The PTTs that were attached to the four partially tracked storks stopped sending signals at various locations in China before the storks' arrivals at wintering sites were confirmed (Table 1).

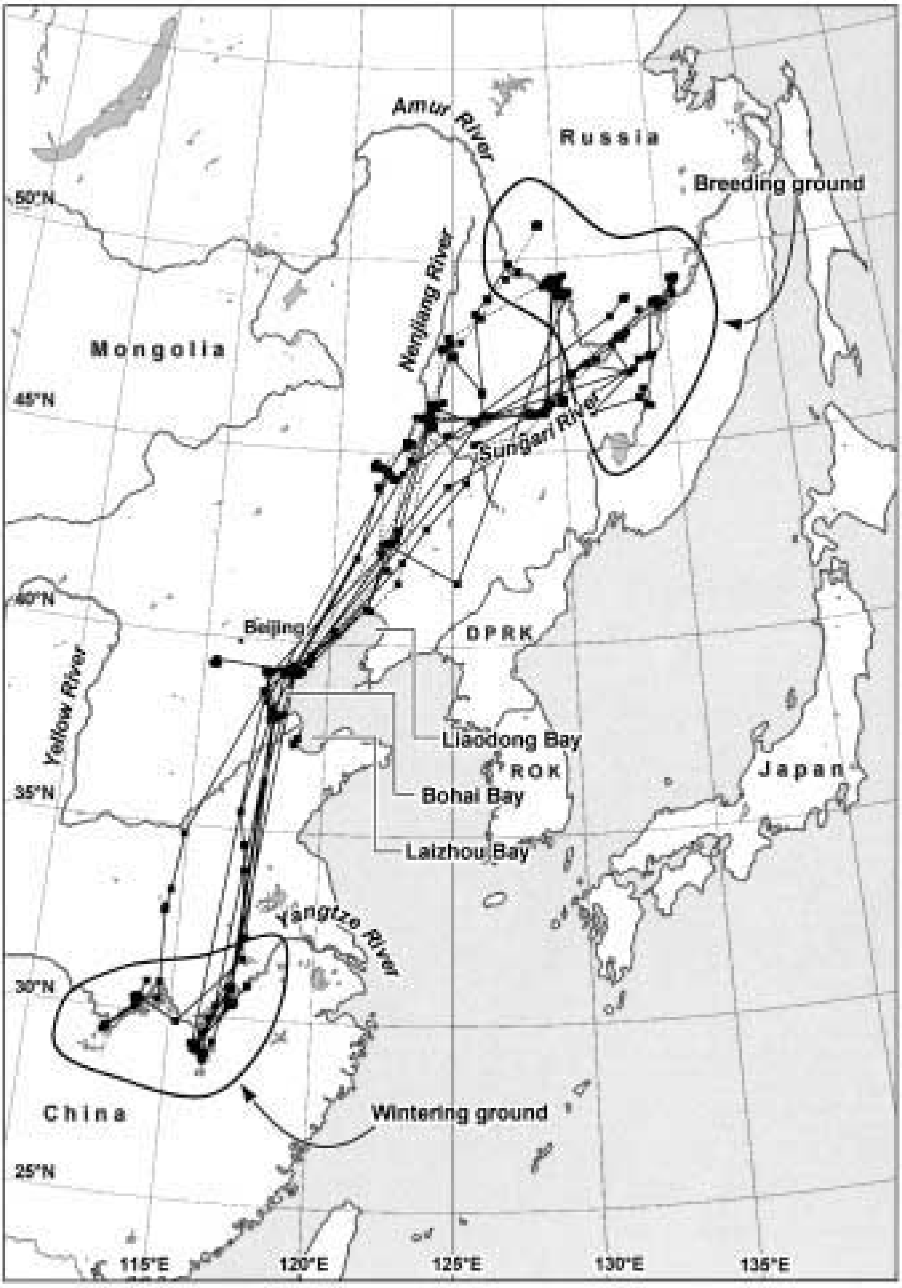


Fig. 2. Autumnal migration routes of the 13 young oriental white storks tracked *via* satellite in 1998 through 2000. Solid lines show the migration routes of the 9 storks that were tracked completely from the Russian Far East breeding (natal) sites to the wintering sites in southeastern China. Dotted lines show the migration routes of the remaining 4 storks that were tracked during a part of their migrations.

The 13 storks generally left their natal sites on the floodplains along the Amur and Ussuri Rivers in the Russian Far East around late August. Up to the middle of October, they traveled southwest or west through dispersed wetland sites along the river systems of the Three Rivers Plain, the Songnen Plain, and the Tongpei Plain in northeastern China. Some of these wetland sites have been reported to be the species' breeding sites (Ma and Jin, 1991). In late October, storks from wetland sites in northeastern China converged at wetland sites along the Bohai Bay seashore in eastern China. By mid-December, most storks had left Bohai Bay and had traveled south to their final destinations, *i.e.*, to Poyang Lake and other neighboring lakes on the floodplain along the middle Yangtze River.

Geographic locations of stopover sites

The appropriate threshold speed for distinguishing the migration state was determined as $T$= 22.6 km/d. By applying this threshold value to the decision rule (1), each location point was assigned to one of four migration states (*i.e.*, "stay", "travel", "arrival", or "departure"). Then, the geographic location and extent of a total of 42 stay sites were identified by specifying the area attainable by a bird moving at 22.6 km/d for one day from the location points labeled as "arrival", "stay", and "departure". Of the 42 stay sites, 27 sites were identified as stopover sites. All 27 stopover sites were located in the range between the storks' natal sites in the Russian Far East and the Laizhou Bay seashore in eastern China (Fig. 3, Table 2).

Important stopover sites

The number of storks visiting and the length of their stay varied widely among the 27 identified stopover sites (Table 2). Among the stopover sites, three wetland sites hosted a relatively high proportion of the 13 storks; the storks also used them for longer periods. Consequently, these three sites, Tonghe Peat Moor (site-ID 21; 46.095°N, 128.942°E), Momoge Nature Reserve (site-ID 20; 45.945°N, 123.939°E), and Jiantuozhi Gley Mire (site-ID 30; 39.221°N, 118.672°E), were regarded as important stopover sites.

Migration period, distance and speed

For the eight storks that reached wintering sites on the Yangtze River floodplain, relevant information on the migration period, the number of stopover sites used during the migration period, the distance traveled, and the mean travel speed are summarized in Table 3. The migration period was defined as the period between the time of the last "departure" point recorded within the breeding (natal) site and the time of the first "arrival" point recorded within the wintering site. The total distance covered by each stork was calculated as the sum of the geodesic distances between the successive stay sites used by each stork.

The eight storks took 59.9 to 116.2 days to complete their autumnal migrations (103.3 $\pm$ 18.2 d, $n$= 8), traveling distances that ranged from 2455 to 3208 km (2759 $\pm$ 243 km, $n$= 8). They made stopovers at three to six sites en route (4.4 $\pm$ 1.1, $n$= 8). We could not calculate the length of stay for all the stopover sites used by two of the eight storks because we failed to specify "arrival" and/or "departure" points within several stopover sites used by the two storks. Excluding these two storks, six of the eight storks spent 73.1 to 82.3% of their total migration time within stopover sites (78.0 $\pm$ 3.3%, $n$= 6). The mean travel speed between stay sites was 87.8 to 170.4 km/d (119.0 $\pm$ 29.6 km/d, $n$= 6); the maximum number of sustained travel days prior to stopping was 4.1 to 9.0 days (6.8 d $\pm$ 1.6, $n$= 6).

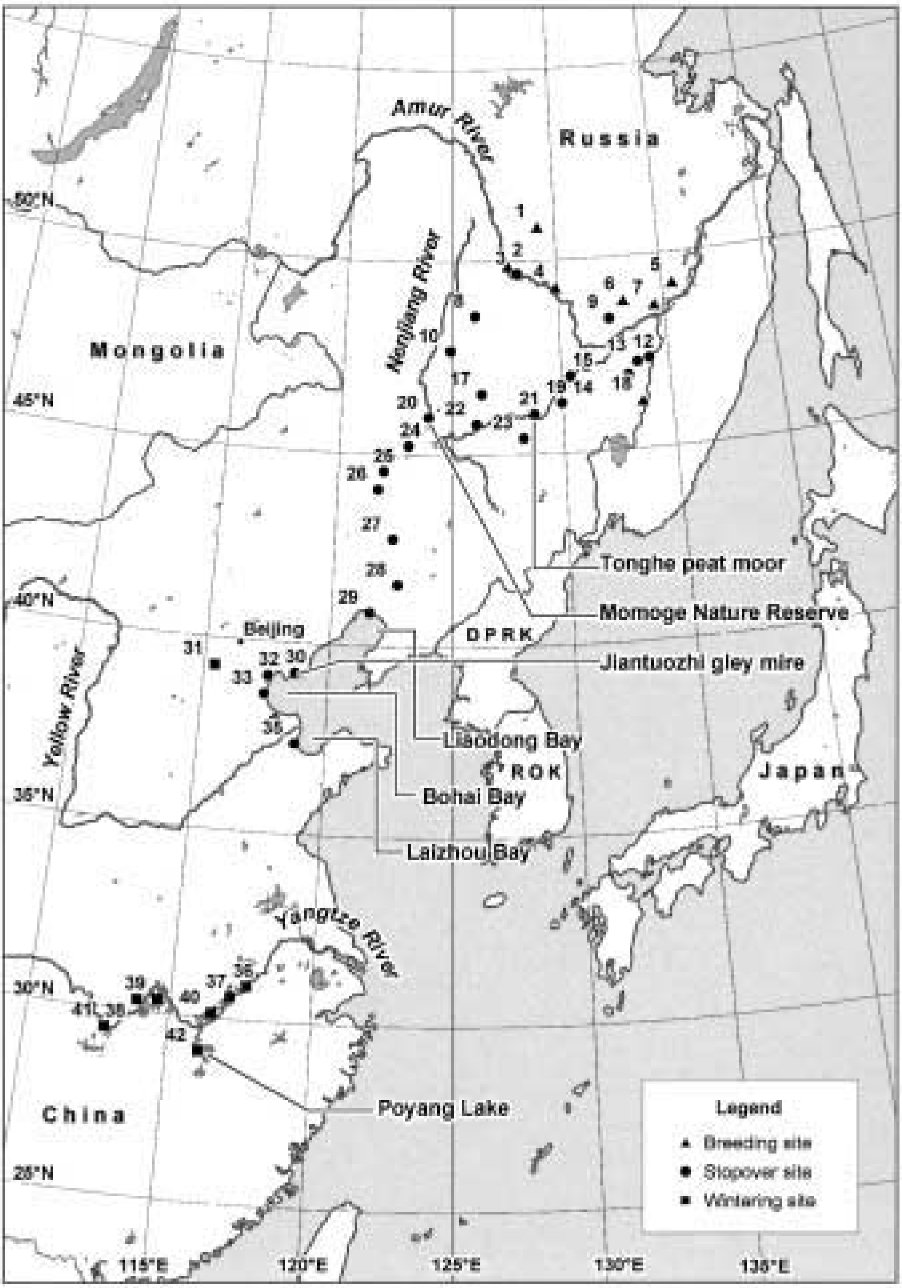


Fig. 3. Geographic locations of breeding (natal), wintering and stopover sites used by the 13 young oriental white storks. The site identification numbers (site-IDs) were appended to the corresponding location.

The accessible distance *D*, which was regarded as the farthest distance that most storks could travel without making stopovers en route, was estimated as 1071 km by multiplying the mean travel speed (119.0 km/d) by the maximum period during which the storks traveled without making a stopover (9.0 d).

Table 2. Geographic coordinates and location of breeding (natal), stopover and wintering sites, and the number of visiting birds and the length of stay for each site used by the oriental white storks tracked from the Russian Far East.

| Site-ID | Latitude | Longitude | Location | Country | Type of use [a] | No. of storks [b] | Stay days [c] |
|---|---|---|---|---|---|---|---|
| 1 | 50.858° N | 129.144° E | The Tom River, about 40 km E of Belgorsk | Russia | B | | |
| 2 | 49.867° N | 127.661° E | The Amur River floodplain, about 50 km SSE of Blagoveshchensk | Russia | B | | |
| 3 | 49.664° N | 128.120° E | The Amur River floodplain, about 85 km SE of Blagoveshchensk | Russia | S | 1 | N/A |
| 4 | 49.263° N | 129.920° E | The Amur River floodplain, about 25 km SW of Arkhara | Russia | B | | |
| 5 | 49.200° N | 135.496° E | The Amur River floodplain, about 70 km NNE of Khabarovsk | Russia | B | | |
| 6 | 48.837° N | 133.111° E | The Amur River floodplain, about 10 km N of Birobidzhan | Russia | B | | |
| 7 | 48.665° N | 134.566° E | The Amur River floodplain, about 40 km WNW of Khabarovsk | Russia | B | | |
| 8 | 48.573° N | 126.074° E | The Nemor He River floodplain, about 200 km NE of Qiqihar | China | S | 1 | 17.8 |
| 9 | 48.395° N | 132.386° E | A branch of the Bidzhan River Floodplain, about 60 km SW of Birobidzhan | Russia | S | 1 | 11.0 |
| 10 | 47.673° N | 124.929° E | Wuyurehe peat moor, about 80 km NE of Qiqihar | China | S | 3 | 30.8 |
| 11 | 47.840° N | 132.812° E | Xinlinchun peat moor on the Three Rivers Plain | China | S | 1 | 19.8 |
| 12 | 47.301° N | 134.097° E | The Ussuri River floodplain on the Three Rivers Plain | China | S | 2 | 7.9 |
| 13 | 47.228° N | 133.562° E | The Qixing River Floodplain, Xinlinchun peat moor on the Three Rivers Plain | China | S | 1 | 2.8 |
| 14 | 47.203° N | 131.176° E | Xinlinchun peat moor on the Three Rivers Plain | China | S | 2 | 5.5 |
| 15 | 46.961° N | 130.422° E | The Sungari River floodplain on the Three Rivers Plain | China | S | 2 | 19.0 |
| 16 | 46.906° N | 133.093° E | Naolihe peat moor on the Three Rivers Plain | China | S | 1 | 2.9 |
| 17 | 46.552° N | 126.339° E | Tongkenhe peat moor, about 90 km NW of Harbin | China | S | 1 | 15.8 |
| 18 | 46.212° N | 133.653° E | Foot in Mt. Wanda Shan | Russia | B | | |
| 19 | 46.277° N | 129.960° E | About 30 km E from Yilan | China | S | 1 | 36.1 |
| 20 | 45.945° N | 123.939° E | Momoge Nature Reserve, Quqihaer gley mire, about 150 km S of Qiqihar | China | S | 5 | 21.4 |
| 21 | 46.008° N | 128.706° E | Tonghe peat moor, about 60 km SW of Tilan | China | S | 4 | 36.4 |
| 22 | 45.779° N | 126.103° E | Haerbin(west) peat moor, about 45 km W of Harbin | China | S | 1 | 17.7 |
| 23 | 45.398° N | 128.194° E | The Mayi River floodplain, about 125 km ESE of Harbin | China | S | 1 | 3.8 |
| 24 | 45.213° N | 123.080° E | Yueliangpao gley mire on the Tongpei Plain, about 45 km SSE of baicheng | China | S | 3 | 10.1 |
| 25 | 44.541° N | 121.992° E | Keerqinzuoyizhongqi gley mire on the Tongpei Plain. | China | S | 3 | 26.3 |
| 26 | 44.075° N | 121.785° E | The Xinkai River floodplain on the Tongpei Plain. | China | S | 1 | 7.1 |
| 27 | 42.783° N | 122.470° E | Upper reaches of Liu He, about 100 km S of Tongliao | China | S | 2 | 15.0 |
| 28 | 41.605° N | 122.715° E | The Liao River floodplain, about 65 km E of Shenyang | China | S | 1 | 3.5 |
| 29 | 40.869° N | 121.594° E | The Shuangtaizi River delta facing Liaodong Bay. | China | S | 1 | N/A |
| 30 | 39.221° N | 118.672° E | Jiantuozhi gley mire facing Bohai Bay | China | S | 11 | 16.7 |
| 31 | 39.281° N | 115.432° E | Yi Xian, about 100 km SW of Beijing | China | W | | |
| 32 | 39.122° N | 117.604° E | Wetland site in Bohai Bay seashore | China | S | 3 | 9.9 |
| 33 | 38.630° N | 117.491° E | Nandagang gley mire facing Bohai Bay | China | S | 2 | 6.2 |
| 34 | 37.976° N | 118.013° E | Dongfenggang gley mire facing Bohai Bay | China | S | 2 | 7.0 |
| 35 | 37.377° N | 118.826° E | Laizhouwan salt swamp facing Laizhou Bay | China | S | 1 | N/A |
| 36 | 30.902° N | 117.667° E | Small lake on the Yangtze River floodplain, near Tongling, | China | W | | |
| 37 | 30.584° N | 117.108° E | Caizi Lake, Dong Lake on the Yangtze River floodplain, near Anqing | China | W | | |
| 38 | 30.297° N | 113.829° E | The Yangtze River floodplain, about 20 km NW of Xintankou | China | W | | |
| 39 | 30.355° N | 114.541° E | Liangzi Lake on the Yangtze River floodplain | China | W | | |
| 40 | 30.125° N | 116.499° E | The Yangtze River floodplain, around Wangjiang | China | W | | |
| 41 | 29.488° N | 112.800° E | Shashi gley mire, Dongting Lake on the Yangtze River floodplain | China | W | | |
| 42 | 29.081° N | 116.139° E | Poyang Lake on the Yangtze River floodplain | China | W | | |

[a] Type of use: B = breeding (natal) sites; S = stopover sites; W = wintering sites.
[b] The number of storks that stayed at the stopover site.
[c] The mean stay days of the storks stayed at the stopover site.

## Site connectedness

The degree of site connectedness of the 27 identified stopover sites ranged from 18 to 34 ($26.9 \pm 4.7$, $n$= 27) (Fig. 4). The Shuangtaizi River delta stopover site (site-ID 29), the Bohai Bay seashore stopover sites (site-IDs 30, 32, 33, and 34), and the Laizhou Bay seashore stopover site (site-ID 35) were less connected than the other sites, suggesting that these regions have relatively few areas of stopover habitat and that, therefore, these coastal areas are critical for maintaining migration route connectivity to north and south.

Table 3. Migration days, travel distance and speed of the 8 storks that wintered on the Yangtze River floodplain in southeastern China.

| PTT-ID | Migration period (MM/DD/YY in GMT) | No. of stopover sites used | Total travel distance (km) [a] | Migration days [b] | Stay days [c] | Travel days [d] | Proportion (Stay/Total) | Max. sustained travel days | Mean travel speed (km/day) [e] |
|---|---|---|---|---|---|---|---|---|---|
| 09086 | 08/20/98 - 12/12/98 | 6 | 2738.2 | 113.8 | 92.0 | 21.9 | 80.8% | 6.2 | 113.7 |
| 20853 | 08/18/98 - 12/09/98 | 3 | 2632.5 | 113.0 | 93.0 | 20.0 | 82.3% | 9.0 | 133.7 |
| 20820 | 08/20/99 - 12/01/99 | 5 | 2989.6 | 105.1 | (g) | (g) | (g) | (g) | (g) |
| 20821 | 09/19/99 - 11/22/99 | 3 | 2455.2 | 59.9 | 43.8 | 16.1 | 73.1% | 4.1 | 170.4 |
| 20823 | 09/07/99 - 12/10/99 | 5 | 3208.5 | 110.0 | (g) | (g) | (g) | (g) | (g) |
| 19033 | 08/15/00 - 12/05/00 | 4 | 2575.0 | 116.2 | 88.1 | 28.1 | 75.8% | 7.0 | 87.8 |
| 19460 | 07/28/00 - 11/09/00 | 4 | 2821.0 | 103.0 | 80.7 | 22.3 | 78.3% | 7.4 | 110.3 |
| 19640 | 07/30/00 - 11/04/00 | 5 | 2651.7 | 105.0 | 81.4 | 23.6 | 77.5% | 7.1 | 98.3 |

[a] The sum of a series of geodesic distances between successive stay sites from the natal site to the first wintering site.
[b] Total number of days elapsed between departure from their natal site and arrival at the wintering site.
[c] The number of days for which storks stayed at stopover sites during the period of their autumnal migrations.
[d] The number of days for which storks traveled between sites during the period of their autumnal migrations.
[e] Mean travel speed is the apparent total travel distance covered during travel days.
[g] These calculations were not available due to prolonged lack of telemetry data.

## Discussion

Most bird migration studies have relied on the banding method for gathering data on the movements of migratory birds. This traditional method requires extensive field investigations in order to resight or recapture the banded birds. The few research programs that have successfully detected movements of individual birds over long distances have been character-

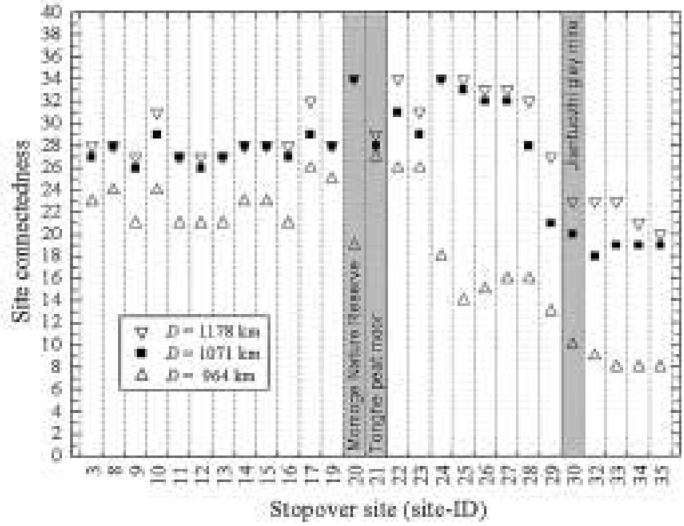


Fig. 4. Site connectedness at each stopover site. To show the influence on the site connectedness by changing the initial assumption ($D$=1071 km), the values changed in either direction by 10% ($D$=1178 and 964 km) were also used in the calculation of the site connectedness.

ized by cooperation among different research teams at widely separated sites and by a choice of species that use a limited number of potential sites (Haig *et al.*, 1998). Satellite tracking is a more effective method for bird migration studies because it can periodically sample the geographic locations of individual birds migrating over a broad spatial scale without extensive field investigations. Our three-year satellite tracking study on the autumnal migrations of oriental white storks provided a basis for understanding the species' migrations; this constituted knowledge that was unattainable by the traditional method.

To accomplish the processes of capture and PTT deployment safely and certainly, we selected fledglings as the targets in our satellite tracking study (Higuchi *et al.*, 2000). Hence, we cannot exclude the possibility that the satellite tracking data we obtained might be biased due to age-stratified migration behaviors. However, because the species has been known to migrate in groups consisting of young and adult birds (Wang, 1991; Wu *et al.*, 1991), the movement patterns exhibited by the young storks are likely to conform to those of adults. Therefore, we assume that the satellite tracking data we obtained are representative of the movements of migrating storks, regardless of their age.

According to previous studies on the foraging ecology of oriental white storks at stopover and/or wintering sites in southeastern China, the species is likely to be diurnal (Wang, 1991; Shi, 1991; Yan, 1991). Therefore, although this is speculative, we assumed that the storks made a short stop during the night, even while they were traveling between stay sites. However, we were not able to identify any short stops from the satellite tracking data due to the inadequate number of location points collected during travel between stay sites.

The 27 stopover sites we identified were thought to be for replenishing nutrient stores, whereas the short stops were not thought to be for feeding. Unless these transitory feeding areas persist, the storks will have great difficulty migrating between the protected areas of their breeding and wintering sites. Especially, the three stopover sites, Tonghe Peat Moor (site-ID 21; 46.095°N, 128.942°E), Momoge Nature Reserve (site-ID 20; 45.945°N, 123.939°E), and Jiantuozhi Gley Mire (site-ID 30; 39.221°N, 118.672°E), which were used for relatively long periods by a relatively high proportion of the 13 storks (Table 2), should receive greater attention as stopover sites important for the conservation of the migratory storks. We will discuss the role of these three important stopover sites in conjunction with their geographic conditions.

Tonghe Peat Moor (site-ID 21) is located along the middle reach of the Sungari River in Heilongjiang Province, northeastern China (Fig. 3). Of the 13 storks we satellite tracked, four stopped here (Table 2). These four had all been fitted with PTTs on the floodplain along the middle reach of the Amur River, near Arkhara in the Russian Far East (site-ID 4). Tonghe Peat Moor was the first stopover site for three storks and the second stopover site for the remaining stork. They spent 28.9 to 43.5 days from late August to early November ($36.2 \pm 7.2$ d, $n$= 4), or approximately 30% of their total migration period, at this site. The storks then flew either southwest (three storks) or west (one stork). The southwestern route included a wetland site (site-ID 30) on the northern shore of Bohai Bay in eastern China. The western route followed the Sungari River and included wetland sites in the Songnen Plain and the Tongpei Plain in northeastern China.

The site connectedness of Tonghe Peat Moor (site-ID 21) was almost equal to the average connectedness of the 27 identified stopover sites (Fig. 4), and the site was within non-stop travel distance of all known breeding sites (Fig. 5a). This accessibility may be one reason the storks selected this site as their first or second stopover site after leaving their natal sites. The southernmost stopover site within the estimated accessible distance ($D$=1071 km) from Tonghe is the Shuangtaizi River delta wetland (site-ID 29). Liaoning Shuangtai Hekou Nature Reserve in this delta has been used as a breeding site for red-crowned cranes (*Grus japonensis*), Saunders' gulls (*Larus saundersi*), and Japanese marsh warblers (*Locustella pryeri*) (Kanai *et al*., 1993). However, the management of the reserve is apparently not adequate to protect the habitat from the development of oil fields within the reserve (Scott, 1989; Kanai *et al*., 1993). For storks traveling directly to the Shuangtaizi site from Tonghe, the degradation of the Shuangtaizi River delta stopover habitat could be an obstacle to their continued travel south. To maintain migration route connectivity, it is recommended that conservation efforts be undertaken at both Tonghe Peat Moor and the Shuangtaizi River delta wetland.

Momoge Nature Reserve (site-ID 20) is situated on the Tongpei Plain, Jilin Province, northeastern China (Fig. 3). This site and its adjacent sites (site-IDs 10, 24, 25, and 26) are situated in a longitudinal row on the Tongpei Plain. This north-south series of stopover sites probably constituted one of the most important southward corridors for the storks, as the sites were utilized by eight of the 13 storks. Momoge Nature Reserve is at the junction of two migration routes: the southern route, taken by storks born west of site-ID 4, and the western route along the Sungari River, taken by storks born east of site-ID 4. The five storks that stayed at Momoge spent 3.1 to 67.3 days there ($22.5 \pm 25.8$ d, $n$= 5), from early August to late October. After resting at this site, two of the five storks moved slowly south, making stopovers at wetland sites in southern Tongpei Plain, and then left for the Bohai Bay wetland sites before the onset of winter. One stork traveled directly to the Shuangtaizi River delta (site-ID 29) facing Liadong Bay. (Further movement is not documented because the PTT

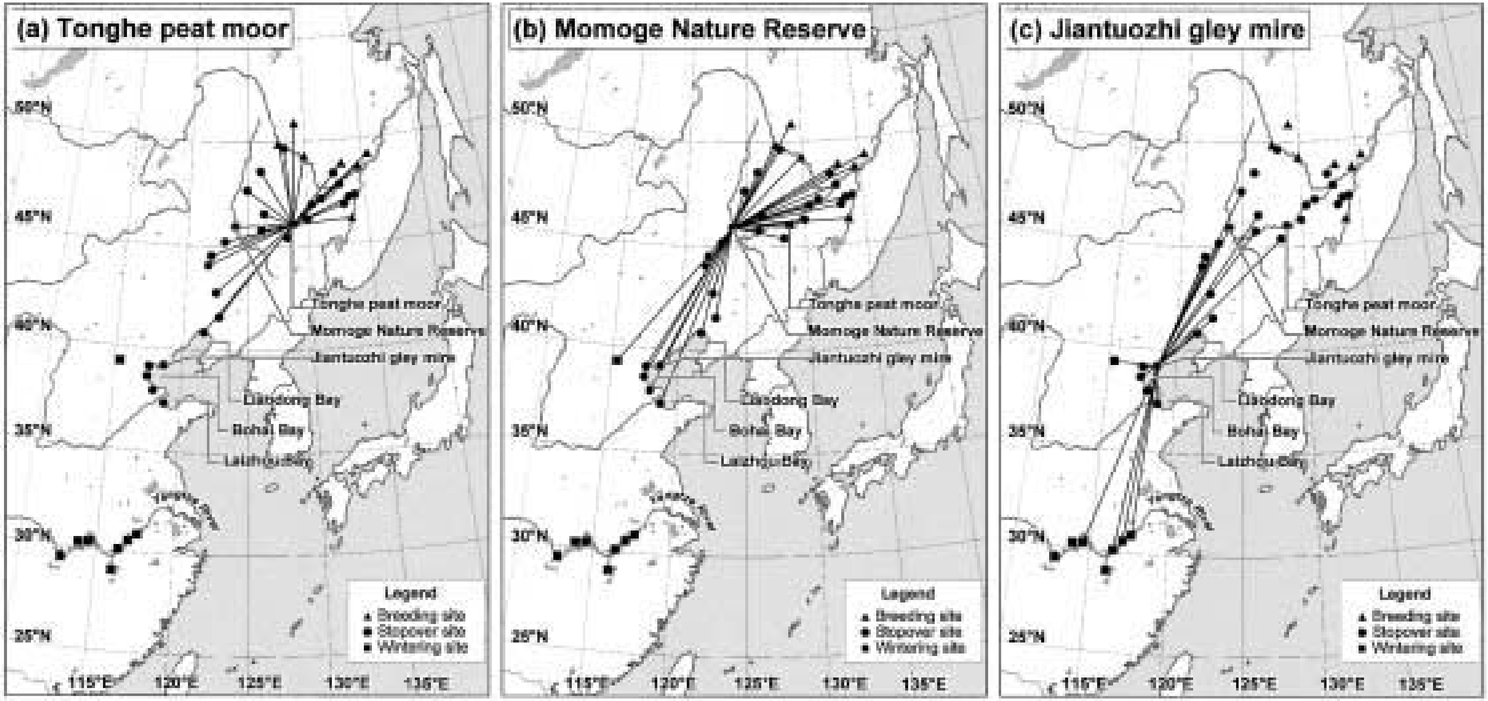


Fig. 5. Accessibility between the important stopover site and its neighboring stay sites. Solid lines indicate the stay sites that are situated within the accessible distance ($D$=1071 km) from the important stopover sites: (a) Tonghe peat moor; (b) Momoge Nature Reserve; and (c) Jiantuozhi gley mire.

stopped signaling at the site.) The remaining two storks stayed within Momoge until the onset of winter and then traveled to the Bohai Bay wetland sites.

The site connectedness of Momoge Nature Reserve (site-ID 20) was the highest among the 27 identified stopover sites (Fig. 4). This nature reserve is accessible by non-stop travel from natal sites, and storks could travel south from this site and reach the Bohai Bay wetland sites without stopping (Fig. 5b). Thus, Momoge Nature Reserve is situated at the optimal location for storks preparing for the autumnal migration toward wintering sites on the Yangtze River floodplain via the Bohai Bay seashore. However, the large-scale development of oil fields in this area has been advancing into the reserve, and the management of the reserve is far from adequate for preserving habitat for migrating storks. The reserve should be managed to maintain wetland conditions as a viable stopover site.

All 12 storks with functional PTTs spent extended periods on the mudflats and wetlands facing Bohai Bay in eastern China (site-IDs 30, 32, 33, and 34). Among these four stopover sites, Jiantuozhi Gley Mire (site-ID 30) was used by 11 of the 12 storks (Table 2). The storks arrived at this site in early November and spent 4.0 to 31.1 days there ($16.4 \pm 10.6$ d, $n$= 9); we could not calculate the length of stay for two storks because we failed to specify their "arrival" and/or "departure" points within the site. They then continued their migration south, arriving, finally, at their wintering sites, Poyang Lake and other neighboring lakes on the floodplain along the middle Yangtze River in southeastern China.

Jiantuozhi Gley Mire (site-ID 30) is the northernmost stopover site in the north within the estimated accessible distance ($D$=1071 km) from the wintering sites on the Yangtze River floodplain. The storks on the southern migration path can travel without stopping from this site to the wintering sites (Fig. 5c). All of the southern stopover sites face Bohai Bay (site-IDs 30, 32, 33, and 34) or neighboring Laizhou Bay (site-ID 35) in eastern China (Fig. 3). The lower site connectedness of these five stopover sites suggests that these sites are at higher risk of being isolated from the migration route network (Fig. 4).

Although Tianjin Wetland and Ancient Coast Nature Reserve was established to protect the wetland ecosystem in the Tianjin municipality on the Bohai Bay seashore (China Population and Environment Society, 2000), this coastal area has been one of the most seriously polluted regions in all China, and the degradation of the costal environment has not yet been effectively controlled. Rapid economic development in this bay area has created intense pressures on the coastal wetland environment. To preserve the connectivity of the storks' migration routes from the breeding sites to the wintering sites, the wetland environment in the coastal areas in eastern China should be managed properly. Especially, Jiantuozhi Gley Mire must have a high priority for protection for two reasons: it is used by many storks, in common, for relatively long periods; and it is at higher risk of being isolated from the migration route network.

## Conclusions

Using satellite tracking, the autumnal migration routes and the geographic locations of stopover sites for the endangered oriental white storks were investigated. In the range between the Russian Far East breeding sites and the wintering sites in southeastern China, 27 stopover sites were identified. Of these sites, the following three stopover sites were identified as the most important, based on the number of visiting birds and the length of their stay:

Tonghe Peat Moor (46.095°N, 128.942°E), Momoge Nature Reserve (45.945°N, 123.939°E), and Jiantuozhi Gley Mire (39.221°N, 118.672°E). These important stopover sites are exposed to threats of development that are linked to economic interests. In addition, as a result of site connectedness evaluation, it could be shown that the stopover sites situated on the seashores of Liaodong Bay, Bohai Bay, and Laizhou Bay in eastern China are less connected than are the other sites. Therefore, among the sites studied, Jiantuozhi Gley Mire on the northern shore of Bohai Bay should have a high priority for protection for two reasons: it is used by many storks, in common, for relatively long periods; and it is at higher risk of being isolated from the migration route network. If this critically located stopover site needs fail to be addressed, many migrating storks will have great difficulty passing between the protected areas of their breeding and wintering sites.

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