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Tracking Migration of Eastern Spot-billed Ducks *Anas zonorhyncha* and Mallards *Anas platyrhynchos* Wintering in Shanghai, China

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Abstract.—Millions of migratory waterfowl winter in the coastal wetlands in Shanghai City, among which Eastern Spot-billed Ducks and Mallards are among the most common species and are sensitive to infection with avian influenza virus. However, information on the migration behaviors of these two species in Northeast Asia is lacking. Therefore, GPS transmitters were used to track the migration of 13 Eastern Spot-billed Ducks and eight Mallards wintering in Shanghai during 2017–2020. Mallards covered a (mean ± standard deviation) migration distance of 1,663.69 ± 1,063.33 km, with wider variation than Eastern Spot-billed Ducks (1,639.24 ± 642.72 km), though the difference was not significant. Both species ended their northward migrations in Northeast Asia encircling the Yellow Sea, mainly in northeastern China. The dynamic Brownian bridge movement model confirmed that multiple stopover sites mainly located in the Korean Peninsula along the Yellow Sea coastline were crucial nodes for maintaining the stability and function of the migration network. This study confirmed the close relationships between habitats in the Korean Peninsula and China, indicating the importance of habitat conservation in related countries to the stability of the migration network. The results of this study additionally highlight the relationships between migration behaviors and outbreaks of avian influenza virus in Northeast Asia. *Received 25 Sept 2022, accepted 13 Apr 2023.*

Key words.—*Anas platyrhynchos*, *Anas zonorhyncha*, Eastern Spot-billed Duck, Mallard, Migration, Satellite tracking, Shanghai

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Shanghai is located in the estuary of the Yangtze River and is the third largest megacity in the world (United Nations Population Division 2018). With a human population of more than 25 million, the rapid urbanization of the city impacts the need for the conservation of 438 recorded bird species, 85% of which are migrants (Cai *et al.* 2011). For example, Shanghai is situated at the midpoint of the East Asian-Australasian Flyway (EAAF), and is thus one of the most important stopovers for migratory waterbirds, with a total wetland area of 3,770 km^2 (Cai and Zhou 2014). Millions of migratory waterbirds are recorded during the nonbreeding seasons each year (Pei *et al.* 2007). However, habitat degradation as a result of the reclamation of coastal wetlands (Ma *et al.* 2014) means that conservation of migratory waterbirds has become an essential ecological issue in Shanghai City (Wang *et al.* 2022), not only in terms of the conservation of local biodiversity, but also for protecting migratory routes and related wild-bird communities.

Many migratory waterbird species are known to be natural hosts of various zoonotic diseases (Olsen *et al.* 2006), and preventing the transmission of avian influenza virus (AIV) from migratory waterbirds to humans and poultry is one of the top biosafety and economic security issues in Shanghai City. Shorebirds and waterfowl (e.g., ducks and geese) are the two main groups of migratory waterbirds (Pei *et al.* 2007), and waterfowl have been identified as the most important group of wild host species of AIV (Shanghai Forestry Bureau 2016; Zhou *et al.* 2016). Basic ecological knowledge, e.g., on the migration of migratory waterbirds, is thus fundamental to addressing both conservation and biosafety issues. However, information on the migration of wintering waterbirds in Shanghai is still limited, especially for waterfowl. Migratory waterfowl usually arrive in Shanghai for wintering from October to November and leave for breeding sites from March to May the next year (Chongming Dongtan National Nature Reserve, unpublished data). Knowledge about their breeding sites, numbers of breeding populations of a specific wintering waterfowl population, and networks among these breeding populations is valuable to the transmission mechanism and the prevention of avian infectious diseases.

The development of satellite tracking technology has made it possible to conduct long-term studies providing accurate and detailed spatial data on the migration of large waterbirds, such as White-naped Cranes (*Grus vipio*), Black-necked Cranes (*Grus nigricollis*), and Whooper Swans (*Cygnus cygnus*; Higuchi *et al.* 1996; Wang *et al.* 2020; Wang *et al.* 2020; Ao *et al.* 2020). In addition, the development of lighter satellite transmitters has recently allowed this technique to be used to study wild ducks (Takekawa *et al.* 2010; Wang *et al.* 2018). Eastern Spot-billed Ducks (*Anas zonorhyncha*) and Mallards (*Anas platyrhynchos*) are two of the dominant wintering waterfowl species in Shanghai City (Pei *et al.* 2007), and have been reported to breed in Northeast Asia (Zhao 2001). The prevalence of AIV reached 24.2% in Mallards and 26.3% in Eastern Spot-billed Ducks (Tang *et al.* 2020). Notably, these two wild duck species are known to be the origins of domestic ducks in eastern China (Li *et al.* 2010), and to utilize artificial habitats and mix with domestic ducks in the coastal areas of Shanghai City (Ye *et al.* 2021). Meanwhile, adults of these two large duck species can weigh up to 1 kg (Zhao 2001). Therefore, their high pathogenicity, sympatric distribution especially to artificial environments, and suitable body sizes make them ideal species for comparative behavioral ecological studies.

In the current study, we tracked the migration behaviors of 13 Eastern Spot-billed Ducks and eight Mallards wintering in Shanghai between 2017 and 2020. We aimed to summarize the migration timings, routes, distances, important stopovers, and breeding sites, and used the data to provide suggestions for the conservation of migratory birds and for preventing the transmission of zoonotic pathogens in heavily urbanized areas like Shanghai City.

METHODS

Study Area

We captured wild ducks in three areas of Shanghai City, including the Dongtan wetland in Pudong District (30°51′–31°06′N, 121°50′–121°51′E), Jiuduansha island (31°06′–31°14′N, 121°46′–122°15′E), and Dongtan wetland on Chongming island (31°25′–31°38′N, 121°53′–122°04′E) covering a total area of 836 km^2. Saltmarsh and mudflat areas, with dominant vegetation comprising *Phragmites australis*, *Scirpus mariqueter*, *S. triqueter*, and invasive *Spartina alterniflora*, are the main coastal wetland habitats of waterbirds at the Yangtze River estuary, Shanghai, China (Pei *et al.* 2007). However, despite being important stopover sites for migratory waterbirds in the EAAF, reclamation has resulted in significant disturbance to these areas (Ma *et al.* 2014; Chen *et al.* 2019).

Bird Capture and GPS Tracker Fixing

Wild ducks were captured using clap nets and placed in cages during field sampling for AIV carried out by the staff from Pu Dong Forestry Station, in January 2017 and 2018 and from October to December 2017–2019. With their permission and supervision, we selected healthy and unwounded Eastern Spot-billed Duck and Mallard adults weighing > 800 g for GPS telemetry. Their species, body mass, and sex were recorded. A 17 g solar-powered GPS-GSM backpack transmitter (model HQBG2715S, Hunan Global Messenger Technology Co., Ltd., Hunan, China) was attached to each duck which fitted the criterion that mounted satellite transmitters should weigh ≤ 3% of the bird's body weight (Wang *et al.* 2018; Kuang *et al.* 2022). The individuals equipped with backpacks were placed into cages for further observation for about 1 hour before releasing.

Telemetry Settings and Data Collection

Each GPS transmitter was scheduled to record the location coordinates, altitude, temperature, speed, course, date and time, voltage, and accuracy of positioning every 6 hours, depending on the battery consumption. The coordinate system was set to WGS 1984. The date and time were recorded in Beijing Time (UTC+8). The quality of the telemetry location coordinates was ranked into six classes: A (SD, 5 m), B (10 m), C (20 m), D (100 m), E (2,000 m), and invalid. We excluded locations ranked as Class E or invalid to control the quality of the data analysis. All valid data were then imported into QGIS 3.16.4 (QGIS Development Team, 2021) for tracking analysis of the migration routes of the ducks.

Migration Parameters

To study the birds' migration behaviors, we identified wintering, stopover, and breeding sites for each tracked individual and calculated the lengths of the segments between the connected stop sites (e.g., wintering, stopover, and breeding sites). Ducks usually moved around during their stay at each stop site. Because all the individuals were captured during their wintering season, we could determine their wintering site during their first tracked northward migration (e.g., the spring migration). However, telemetry data transmission can be terminated for technical reasons or if the tracked individual dies. It was therefore not possible to confirm the exact breeding sites for individuals during the northward migration or the wintering sites for individuals during the southward migration (e.g., the autumn migration) if the telemetry data transmission was terminated. To control the accuracy of identifying each stop, we therefore defined the breeding and wintering sites for a tracked duck according to our tracking data, as the areas at the two ends of each detected migration in which the individual stayed continuously for at least 30 days before or after the migration, with no movement > 100 km in any particular direction (Tajiri *et al.* 2015; Wang *et al.* 2018). Stopover sites were defined as temporary resting areas where birds stayed continuously for ≥ 7 days during their migrations (Si *et al.* 2018). Only the main resting areas during the migration were therefore involved. We then generalized essential migration routes according to the geographic similarities of the wintering, stopover, and breeding sites among the tracked ducks. The migration distance for each duck was calculated as the sum of the lengths of the segments between successive stops. The first flight distance was defined as the distance between the wintering (or breeding) site and the first stop (Kuang *et al.* 2020).

We estimated the time of departure and arrival of each duck at the wintering, stopover, and breeding sites as follows. If the time interval between two consecutive GPS locations before and after leaving the stop site was < 24 hours, the time of the last recorded location at the stop site was used as the departure time. If the time interval between two consecutive GPS points before and after arriving at the stop was < 24 hours, the arrival time was considered according to the first recorded location at the stop site. If it was > 24 hours, the departure and arrival times were defined as the average time between two consecutive data points before and after leaving or arriving at the stop, respectively (Giunchii *et al.* 2018). We considered the migration duration of each tracked duck as the period from the day of departure from the wintering site to the day of arrival at the breeding site, and vice versa (Wang *et al.* 2018). The duration spent at each stopover site was calculated for each migrant duck (Si *et al.* 2018).

Some tracking data were inevitably missing as a result of low battery power or poor GPS or GSM signals. To bridge these gaps, when GPS data missing during the migration, we hypothesized that the tracked ducks moved in a straight line between the two consecutive recorded locations. Some individuals lost their signals when staying at a last recorded stop site < 30 days during the migration. We defined these stops as terminals of their migration but their breeding sites were judged as unknown. Data of these individuals were excluded from further analyses when complete migration data are needed.

Data Analysis

Differences in migration behaviors were tested between the two species, sexes, and individuals with different migration strategies. Migration distances were compared between species and between individuals within each species that used and did not use stopovers using Welch's two sample t-test. Differences in departure dates from wintering sites and arrival dates at breeding sites were compared between the species using Wilcoxon's rank sum test, defining the earliest date at which an individual started migration as 0, and all the other ducks were then ranked according to the number of days between their departure date and the earliest departure date. Wilcoxon's rank sum test was also used to compare the number of stopover sites used and time spent at stopover sites by ducks from the two species. The correlation between the number of stopovers and migration distance was analyzed by Spearman's rank correlation. There was substantial bias between the numbers of male and female individuals for both duck species (Table 1, S1), and no statistical analysis was therefore carried out between the sexes.

Finally, to evaluate the coverage of flyways of the two duck species, we calculated the utilization distribution (UD) through the dynamic Brownian bridge movement model (dBBMM) using the 'move' package (Kranstauber *et al.* 2012). We estimated the 99%, 97%, and 95% UDs cumulative probability contours for all tracked birds and each species by setting a grid resolution of

Table 1. Statistics of stopover sites use and migration distances between the two duck species based on individuals with complete migration data ($\bar{x}$ ± SD). Route 1: eight Eastern Spot-billed Ducks (male:female, 2:6), three Mallards (0:3); Route 2: two Eastern Spot-billed Ducks (male:female, 0:2), three Mallards (1:2).

Species	Departure date (days)			Arrival date (days)			Stopover sites*		Northward migration distance (km)*				
	Total	Male	Female	Total	Male	Female	*n* sites	Duration (days)	Total	Route 1#	Route 2#	With stopover sites	Without stopover sites
Eastern Spot-billed Duck	*n* = 10 14 Apr ± 25	*n* = 2 25 Mar ± 9	*n* = 8 20 Apr ± 25	9 May ± 30	8 Apr ± 5	6 May ± 26	0.6 ± 0.7	17 ± 16	1,639.24 ± 642.72	1,853.41 ± 535.70	782.55 ± 10.91	2,090.53 ± 366.06	1,087.95 ± 290.39
Mallard	n = 6 25 Mar ± 21	n = 1 20 Mar	n = 5 26 Mar ± 20	20 Apr ± 30	21 Mar	26 Apr ± 28	0.9 ± 0.8	21 ± 21	1,663.69 ± 1,063.33	2,684.28 ± 344.43	643.10 ± 243.96	2,684.28 ± 344.43	643.10 ± 243.96
	W= 46.0			W=35.5			W = 26.5	W=23.50	$t_{7.074}$ = -0.04		$t_{13.627}$ = 6.310, P < 0.001		
	P= 0.09			P= 0.59			P = 0.72	P=0.49	P = 0.96				

100 km^2, a window size of 31 locations and margins of 11 locations (Palm *et al.* 2015; Si *et al.* 2018).

All of the above analyses were conducted in R 4.1.2 (R Development Core Team 2021).

RESULTS

A total of 72 captured wild ducks were equipped with GPS-GSM transmitters, including 52 Eastern Spot-billed Ducks and 20 Mallards, among which northward migration data were recorded from 21 individuals, including 13 Eastern Spot-billed Ducks (male:female 3:10; ESPD001–ESPD013) and eight Mallards (2:6; MALL001–MALL008; Table S1). We collected 20,354 GPS positions as of 28 February 2021, of which 19,831 (97%) were qualified. Nineteen of the 21 tracked individuals wintered in Shanghai, while two birds (ESPD012 and MALL001) captured in Shanghai wintered in Zhoushan Archipelago, which is in the vicinity of Shanghai (Fig. 1, 2).

Northward Migration Routes and Schedules

All 21 migrant individuals started their northward migrations from the coastal wetlands of Shanghai and the nearby islands (e.g., Zhoushan Archipelago). Most migrations ended in Northeast Asia around the Bohai Sea and the Yellow Sea, mainly in northeastern China and the Korean Peninsula. Northeastern China, including Liaoning, Jilin, and Heilongjiang provinces, and the eastern part of the Inner Mongolia Autonomous Region, were the destinations of the northward migrations for 71% (15/21) of the tracked ducks (Table S1). In summary, both Eastern Spot-billed Ducks and Mallards followed two main northward migration routes (Fig. 1, 2): (1) northward migration route 1, starting from Shanghai (and islands in the vicinity) and ending in Northeast Asia (Fig. 1a-c, 2a, 2b), and (2) northward migration route 2, starting from Shanghai (and islands in the vicinity) and ending in Jiangsu Province and Shandong Province, eastern China (Fig. 1d, 2c).

Eleven Eastern Spot-billed Ducks and five Mallards flew northward migration route 1

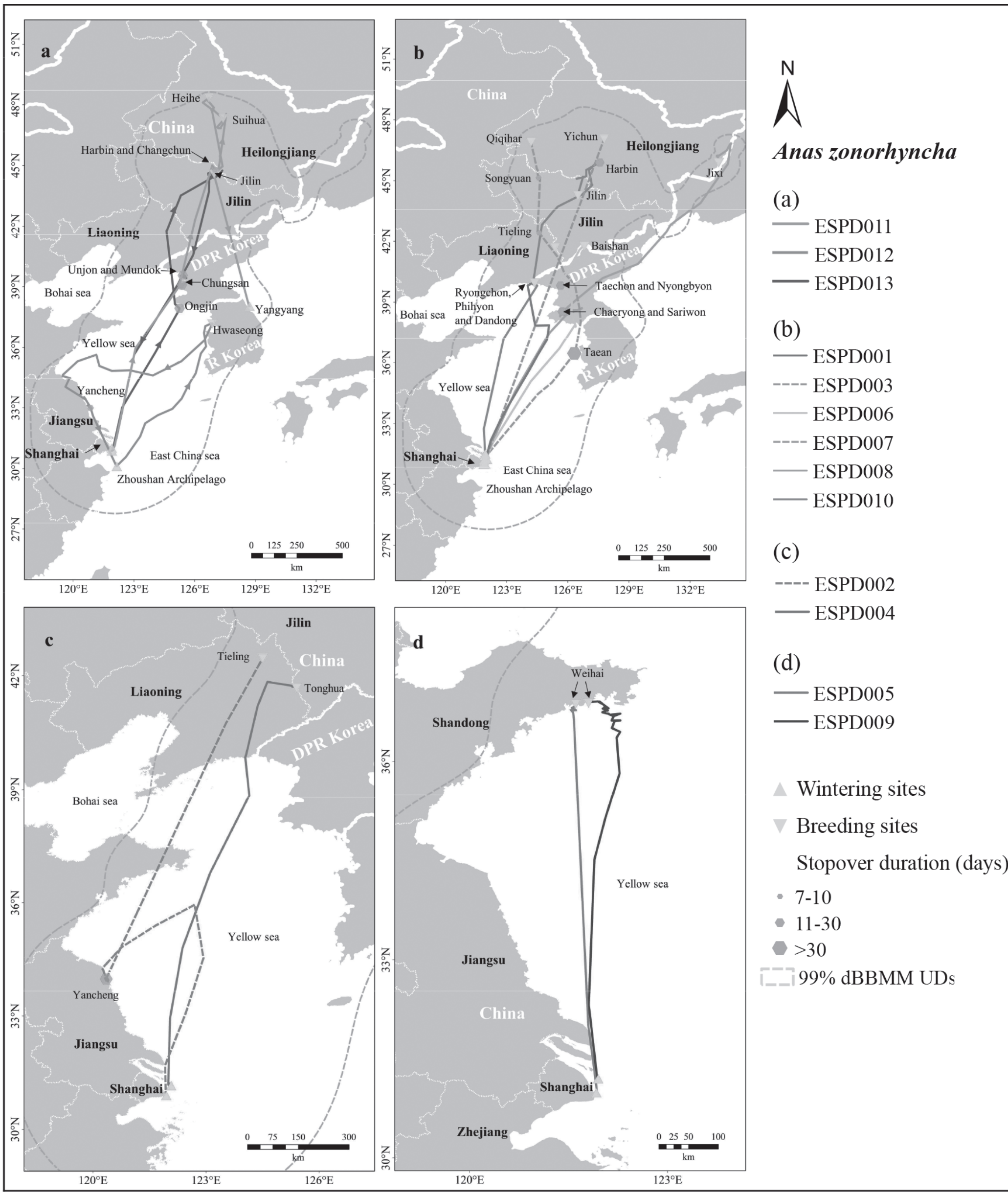

Figure 1. Migration routes and important stopover sites of Eastern Spot-billed Ducks (*Anas zonorhyncha*): year-round routes of three Eastern Spot-billed Ducks (a), northward migration route 1 (b, c), and northward migration route 2 (d). The regular and inverted triangles represent wintering and breeding sites respectively; hexagons show individual stopover sites and their size corresponds to stopover duration. The solid lines show the complete northward migration routes and three complete southward migration routes and dashed lines show incomplete northward migration routes due to the loss of signals. The gray dashed contour represents the area of the 99% utilization distribution calculated by the dynamic Brownian bridge movement model (dBBMM UDs). DPR Korea, Democratic People's Republic of Korea; R Korea, Republic of Korea.

(Figs. 1, 2, Table S1). Among them, complete GPS data were collected from eight Eastern Spot-billed Ducks and three Mallards. Except ESPD012, all the other ten individuals ended their northward migrations by staying in breeding sites in northeastern China, including ESPD001 stayed at the Yalu River estuary and moved regularly between

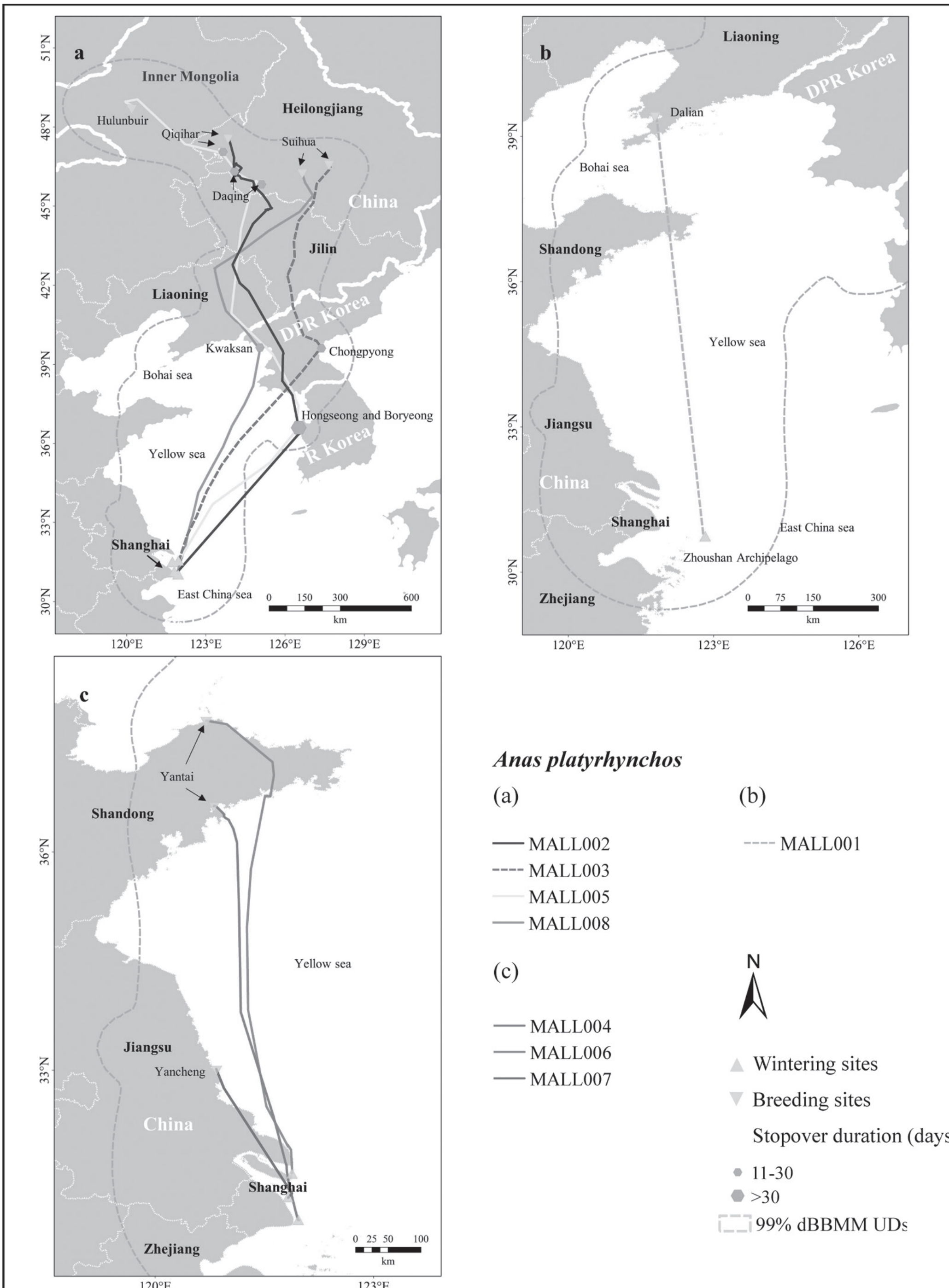

Figure 2. Migration routes and important stopover sites of Mallards (*Anas platyrhynchos*): northward migration route 1 (a, b), and northward migration route 2 (c). The regular and inverted triangles represent wintering and breeding sites respectively; hexagons show individual stopover sites and their size corresponds to stopover duration. The solid lines show the complete northward migration routes and dashed lines show incomplete northward migration routes due to the loss of signals. The gray dashed contour represents the area of the 99% utilization distribution calculated by the dynamic Brownian bridge movement model (dBBMM UDs). DPR Korea, Democratic People's Republic of Korea; R Korea, Republic of Korea.

areas across the border between the Democratic People's Republic of Korea (DPRK) and China (Fig. 1b, Table S1). The mean migration distance for Eastern Spot-billed Ducks was 1,853.41 ± 535.70 km (± SD), with a mean first flight distance of 1,211.84 ± 354.40 km, which accounted for 71% ± 26% of their entire northward migration distance. The mean northward migration distance for Mallards was 2,684.28 ± 344.43 km, with a mean first flight distance of 1,335.63 ± 602.77 km, accounting for 48% ± 16% of their entire northward migration distance (Table 1, S1). Mallards flew longer than Eastern Spot-billed Ducks during the entire migration and first flight, though statistical analysis was not valid because of extremely biased sampling sizes between the two species (Table 1). To the other five individuals without complete GPS data (Table S1), their north migration distances cannot be calculated, because of unconfirmed migration ends due to data durations < 30 days at their last stops (ESPD002, ESPD003, ESPD007, MALL003) and missing GPS signals during the migration (ESPD003 and MALL001).

Only five ducks from the two species followed northward migration route 2 (Fig. 1d, 2c, Table S1). Two Eastern Spot-billed Ducks (ESPD005 and ESPD009) and two Mallards (MALL004 and MALL006) flew directly to their breeding sites in Shangdong Province. The total migration distance of each of the four ducks was < 900 km (Table S1). MALL007 migrated to Yancheng, Jiangsu Province, which was only about 301 km north of the wintering site in Shanghai, and stayed there until December 2020 before its signal was lost. Migration distances of ducks following route 2 were significantly shorter than ducks following route 1 ($t_{13.627} = 6.310$, $P < 0.001$, Table 1).

Based on the complete migration data from ten Eastern Spot-billed Ducks and six Mallards (Table 1), migration behaviors between the two duck species were compared. No significant difference was detected between Eastern Spot-billed Ducks and Mallards in departure ($W = 46.0$, $P = 0.09$) and arrival times ($W = 35.5$, $P = 0.59$). However, in both species, the male tended to start and finish their northward migrations ahead of the female, though statistical tests were not valid because of the extreme bias in the sex ratio of tracked ducks (Table 1). There was also no significant difference in the length of the northward migration between the two species ($t_{7.074} = -0.047$, $P = 0.96$), but Mallards (1,663.69 ± 1,063.33 km) tended to show a wider variation than Eastern Spot-billed Ducks (1,639.24 ± 642.72 km, Table 1).

Year-round Migration Routes

We observed the complete year-round migration behaviors, including the northward and southward migrations, in three Eastern Spot-billed Ducks (ESPD011, ESPD012, and ESPD013) in a large area including eastern China and Northeast Asia (Fig. 1a, Table S1). ESPD011 wintered in Shanghai and migrated north to the breeding site in Suihua, Heilongjiang Province, and then migrated south to winter in Yangyang, Republic of Korea (ROK) with a total year-round migration distance was 3,855.12 km. ESPD012 started northward migration from Zhoushan Archipelago to the breeding site at Hwaseong, ROK, and then flew south to winter in Shanghai with a total migration distance of 2,897.83 km. ESPD013 departed the wintering site in Shanghai and stayed in Jilin, Jilin Province during the breeding season, and then returned to Shanghai for wintering, covering a total distance of over 3,940.17 km (Table S1).

Stopover Sites

During the entire research period, a total of 16 stopover sites were identified to be used by seven Eastern Spot-billed Ducks (11 sites) and four Mallards (five sites; Table S1). All these stopover sites were used by individuals migrating through northward migration route 1 and the coming southward migration (Table S1). Most stopover sites were located in the Korean Peninsula. Six Eastern Spot-billed Ducks and three Mallards used a total of nine stopover sites in the Korean Peninsula, including seven in the DPRK and two in ROK (Fig. 1, 2, Table S1,). All of these, except for Chongpyong (DPRK), were located on the west coast of the peninsula. In contrast, three Eastern Spot-billed Ducks and two Mallards used six stopover sites in northeastern China and two Eastern Spot-billed Ducks used one stopover in Yancheng, Jiangsu Province, eastern China (Fig. 1, 2, Table S1).

There were no significant differences in the number of stopover sites (W = 26.5, P = 0.72) and duration at all the stopover sites (W = 23.5, P = 0.49) used by each individual between the two species (Table 1). However, migration distances of individuals with stopover sites were significantly longer than those without using stopover sites in both duck species (Table 1). The number of stopover sites used was positively correlated with migration distance for both Eastern Spot-billed Ducks (σ = 0.83, P = 0.002) and Mallards (σ = 0.925, P = 0.008).

Flyway estimation by dBBMM

A flyway area of 2.146×10^6 km^2 at the 99% dBBMM UD level was calculated based on the migration GPS data of 21 ducks, which covered almost entire area of Bohai Sea and the Yellow Sea, including an area of 1.344×10^6 km^2 of the land enclosing the sea (Table 2). Directional flyway maps were even more clearly depicted by dBBMM 97% and 95% UDs, from eastern China (e.g., Shanghai and Jiangsu Province) to northeastern China (Fig. 3a).

Land use simulation for each duck species revealed a larger flyway area of Eastern Spot-billed Ducks than Mallards at all three UD levels (Table 2). Moreover, 97% and 95% UDs further confirmed important stop sites (i.e., wintering, stopover, and breeding sites identified) and areas for both species around Bohai sea and Yellow sea and in northeastern China (Fig. 3b, 3c).

Discussion

In this study, we revealed the migration behaviors of two common wild duck species, Eastern Spot-billed Ducks and Mallards, in Northeast Asia around the Yellow Sea. Our data suggested that both species wintered in Shanghai and the nearby islands and migrated north, mainly ending in north-

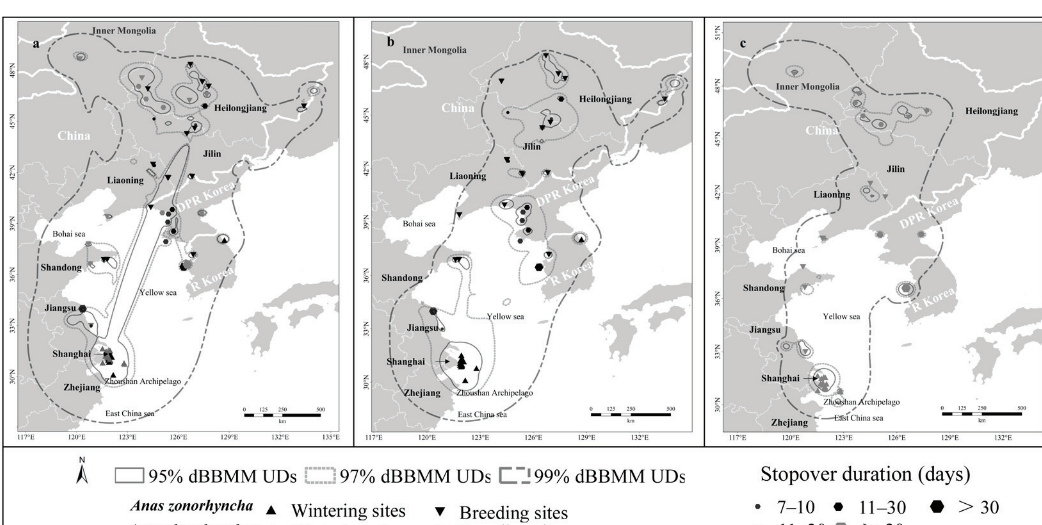

Figure 3. The utilization distribution of all individuals (a), Eastern Spot-billed Ducks (Anas zonorhyncha) (b) and Mallards (Anas platyrhynchos) (c), shown by the 95% (black solid lines), 97% (grey dashed lines) and 99% (black dashed lines) volume contours from the dynamic Brownian bridge movement model (dBBMM UDs). Black and grey symbols represent the stops of Eastern Spot-billed Ducks and Mallards respectively: the regular and inverted triangles indicate wintering and breeding sites respectively; the hexagons show individual stopover sites and their size corresponds to stopover duration (days). DPR Korea, Democratic People's Republic of Korea; R Korea, Republic of Korea.

eastern China. Moreover, multiple stopover sites during migration, including wetlands in eastern China and the Korean Peninsula along the Yellow Sea coast, appear to be crucial nodes to maintaining the stability and function of the migration network. As the dominant waterfowl species in the Yangtze River estuary, basic data on the migration behaviors of these species will provide vital information for both conservation biology, and also in relation to ecological security.

Although Mallards have a much wider global distribution than Eastern Spot-billed Ducks (Ma and Chen 2018), their migration routes (Fig. 1, 2) and space use (Fig. 3) are largely overlapped in eastern China and Northeast Asia as revealed by this study. However, with the similar average northward migration distances, Mallards showed a wider standard deviation than Eastern Spot-billed Ducks (Table 1), indicating more scattered breeding sites used by Mallards than Eastern Spot-billed Ducks. This difference was clearly demonstrated by areas of UDs evaluated by dBBMM that larger but more concentrated core habitat areas used by Eastern Spot-billed Ducks (Fig. 3b) than Mallards (Fig. 3c) in their breeding sites in Northeast Asia (Table 2).

Long-distance migration consumes a lot of energy, and birds thus need to reserve fat before departure and/or refuel during migration (Zheng 1995; Si *et al.* 2018). Our data showed that tracked individuals of both species that used stopover sites flew significantly further than individuals that did not use such sites (Table 1, S1). The results showed that the first flight made by the ducks after leaving their wintering sites for their breeding sites was the longest of all the consecutive flights, accounting for over half of the total migration distance in individuals of both species. Energy storage at the wintering sites is therefore essential for a successful migration. However, fat deposits may not be adequate to allow the birds to reach their destination as migration distances increase; indeed, only half of the individuals with complete tracking data finished their migration by direct flights. Eastern Spot-billed Ducks and Mallards were observed to employ a

Table 2 Areas utilization distributions of flyways using dynamic Brownian bridge movement models.

	Areas of Total dBBMM UDs (km^2)			Areas of dBBMM UDs on land (km^2)		
	99%	97%	95%	99%	97%	95%
Eastern Spot-billed Ducks (n = 13)	1,537,263.45	383,973.81	90,863.23	891,098.77	207,408.74	45,133.44
Mallards (n = 8)	1,171,257.29	109,812.52	33,194.21	723,848.02	76,116.86	19,337.86
All individuals (n = 21)	2,146,486.78	454,055.05	243,613.80	1,344,044.26	248,474.43	114,843.43

"long-stay and short-travel" spring migration (e.g., northward migration) strategy (Yamaguch *et al.* 2008; Si *et al.* 2018), and both species tended to spend most of their time at stopovers, where they stayed for ≥ 7 days before flying directly to their final breeding areas in 1–3 days (Table S1). Food resources along the migration route are thus essential to enable the migrants to reach their destination, irrespective of whether they fly directly or use stopover sites to refuel.

Consistency of bird-migration patterns (including schedules, routes, and stopovers) has frequently been discussed. Birds from the same population can utilize similar or completely different migration paths during their spring and autumn migrations, largely because of variations in the climate, phenology (Vansteelant *et al.* 2017; Briedis *et al.* 2018), food resources, and human disturbance (Boer *et al.* 2011; Hua *et al.* 2015). Indeed, our observations of the northward migration behaviors of the two duck species revealed that various wintering, stopover, and breeding sites were used by different individuals. Moreover, the three Eastern Spot-billed Ducks with full year-round migration data showed different northward and southward migration flyways, although two of them went back to the same wintering sites. However, all these flyways (except for the southward migration of ESPD011) can be categorized into two migration routes and all went via the Yellow Sea. The two wintering sites (Shanghai and Zhoushan Archipelago), most stopover sites, and several breeding sites belonging to eastern China and the Korean Peninsula encircle the Yellow Sea. These results suggested that, although the exact flyway of each individual duck may be different, the general Pan-Yellow Sea migration routes were stable. Consequently, protecting habitats along the coastline of the Yellow Sea is essential to the conservation of migratory birds. However, Chinese eastern coastal areas have recently been subject to multiple disturbances, including excessive reclamation of mudflats, invasion by alien plant species, and human activities, resulting in serious habitat loss and degradation (Boer *et al.* 2011; Hua *et al.* 2015). Wang *et al.* (2022) reported that habitat loss at one stopover site is unlikely to be compensated for by other sites along the Yellow Sea coastline. Protecting existing important stop sites (including wintering, stopover, and breeding sites) is therefore crucial for the conservation of the migration network of waterfowl.

In addition to the conservation issues, the probability of long-distance movements of migrating animals enhancing the spread of zoonotic pathogens from wildlife to humans and human-related animals has concerned academia and the public (Altizer *et al.* 2011). Both Eastern Spot-billed Ducks and Mallards have been recognized as important wildlife host species of AIV (Olsen *et al.* 2006), which is a zoonotic disease with high public security priority in Shanghai City. Eastern Spot-billed Ducks were one of the main wildlife host species during the outbreak of HPAI H5N8 in wild birds in Shanghai during 2013 to 2014. Molecular and epidemiological analyses suggested that this novel AIV strain was highly related to the virus reported in ROK (Zhou *et al.* 2016). However, little empirical information was available at that time on wild waterfowl migration routes from wetlands at the Yangtze River estuary to other Northeast Asian countries to provide an ecological link to transmission of the highly pathogenic HPAI H5N8 strain. The current study demonstrated the close relationships among stopover sites encircling the Yellow Sea, including in China and the Korean Peninsula, especially for the three Eastern Spot-billed Ducks with available year-round tracking data. An *et al.* (2021) recently studied HPAI AIV in poultry in ROK and confirmed the importance of poultry ducks in the spread of the virus. Moreover, the areas most vulnerable to HPAI AIV epidemics were all located in the western part of the Korean Peninsula (An *et al.* 2021), with extensive overlap with stopover and breeding sites for Eastern Spot-billed Ducks and Mallards on the peninsula (Fig. 3). Knowledge about the migration network of waterfowl between China and the Korean Peninsula thus furthers our understanding of the epidemiology of zoonotic diseases in this region. To the prevention of AIV and other avian infectious diseases in

Shanghai City, stopover and breeding sites confirmed in this migration network are all "outposts" which can provide essential chronological and spatial information about circulating strains of pathogens. Meanwhile, since a wintering duck population in Shanghai is a combination of individuals belonging to several populations in breeding sites, recombination and mutations of pathogens in relevant migratory water birds in Shanghai need further concern. In summary, this migration network implicates the importance of international cooperation in the joint surveillance of zoonotic diseases especially transmitted by migratory species in large space scale.

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