K et al. Avian Res (2020) 11:24
:// . /10.1186/ 40657-020-00210-

Avian Research

RESEARCH

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Abstract

Background: Conserving migratory birds is challenging due to their reliance on multiple distant sites at di□erent stages of their annual life cycle. The concept of "flyway", which refers to all areas covered by the breeding, nonbreeding, and migrating of birds, provides a framework for international cooperation for conservation. In the same flyway, however, the migratory activities of the same species can di□er substantially between seasons and populations. Clarifying the seasonal and population di□erences in migration is helpful for understanding migration ecology and for identifying conservation gaps.

Methods: Using satellite-tracking we tracked the migration of Whimbrels ( ) from nonbreeding sites at Moreton Bay (MB) and Roebuck Bay (RB) in Australia in the East Asian–Australasian Flyway. Mantel tests were used to analyze the strength of migration connectivity between the nonbreeding and breeding sites of MB and RB populations. Welch's test was used to compare the migration activities between the two populations and between northward and southward migration.

Results: During northward migration, migration distance and duration were longer for the MB population than for the RB population. The distance and duration of the first leg flight during northward migration were longer for the MB population than for the RB population, suggesting that MB individuals deposited more fuel before departing from nonbreeding sites to support their longer nonstop flight. The RB population exhibited weaker migration connectivity (breeding sites dispersing over a range of 60 longitudes) than the MB population (breeding sites concentrating in a range of 5 longitudes in Far Eastern Russia). Compared with MB population, RB population was more dependent on the stopover sites in the Yellow Sea and the coastal regions in China, where tidal habitat has su□ered dramatic loss. However, RB population increased while MB population decreased over the past decades, suggesting that loss of tidal habitat at stopover sites had less impact on the Whimbrel populations, which can use diverse habitat types. Di□erent trends between the populations might be due to the di□erent degrees of hunting pressure in their breeding grounds.

Conclusions: This study highlights that conservation measures can be improved by understanding the full annual life cycle of movements of multiple populations of Whimbrels and probably other migratory birds.

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Keywords: Conservation, Flyway, Migration, Migration connectivity, Stopover, Tracking, Yellow Sea

Background

e annual life cycle of migratory birds depends on distant breeding, nonbreeding, and stopover sites as well as the interlinkage shaped by these sites (Newton 2008). e concept of "flyway", which refers to all of the areas covered by breeding, nonbreeding, and migrating of birds, provides a framework for international cooperation in the conservation of migratory birds and their key areas (Boere and Stroud 2006). Over the past decades, field surveys have identified many key areas used by migratory birds, which has facilitated the designation of conservation hotspots along a flyway (e.g., Bamford et al. 2008). However, the temporal and spatial patterns of migration can be quite di erent between seasons and between populations of the same species in the same flyway (e.g., Battley et al. 2012; Hewson et al. 2016). Understanding the seasonal and population di erence in migration activities can be helpful for detecting the factors linked with population dynamics, for finding conservation gaps, and for developing targeted conservation measures.

Geographical distribution greatly a ects the temporal and spatial patterns of migratory populations. In general, the higher the latitude of the breeding site, the later the suitable time to initiate breeding (especially for those species breeding in the Arctic which must wait for snow melt), and thus the later the birds depart from nonbreeding sites and arrive at breeding sites (Conklin et al. 2013; Briedis et al. 2016). With an increase in nonstop flight distance, birds require a longer time to deposit more fuel to support migratory flight before departure (Conklin et al. 2013; Zhao et al. 2017). Moreover, migratory routes are closely linked with the availability and quality of stopover sites. e quality of stopover sites can a ect the population dynamics of migratory birds. For example, a decline in the numbers of the Common Cuckoo (*Cuculus canorus*) that breed in the UK is related to the use of the western migration route, which provides low quality habitat (Hewson et al. 2016). In the East Asian–Australasian Flyway (EAAF), the rapid population decline of many migratory shorebirds is related to the dramatic habitat loss and degradation at their critical stopover sites in the Yellow Sea (Hua et al. 2015; Piersma et al. 2016; Studds et al. 2017).

Migration routes and stopover sites can also di er between the northward and southward migration of the same population. Weather conditions, especially wind conditions, influence the seasonal di erence in migration activities (Alerstam et al. 2003). Because flying with a tailwind reduces fuel consumption and increases migration speed, birds prefer to use migration routes that provide tailwind assistance, and seasonal di erences in wind direction and strength may therefore greatly a ect migration routes and stopover decisions (e.g., Shamoun-Baranes et al. 2017; Carneiro et al. 2019). Migration can also be a ected by the activities after arrival at the migration destination. Because breeding activities are time-constrained, migratory birds face great time pressure during migration to their breeding grounds. As a consequence, for boreal breeding species, birds generally exhibit shorter stopover durations, and thus faster migration speeds, during northward than southward migration (Battley et al. 2012; Nilsson et al. 2013; Zhao et al. 2017).

In recent years, many migratory shorebirds in the EAAF have su ered rapid population decline (Hua et al. 2015; Piersma et al. 2016; Studds et al. 2017). Clarifying the full annual life cycle of movements is the basis for identifying potential causes of these declines and conservation gaps. e Whimbrel (*Numenius phaeopus*) is a long-distance migratory shorebird with a worldwide distribution. In the EAAF, there are about 65,000 individual Whimbrels (Hansen et al. 2016), and these belong to the subspecies *N. p. variegatus* (Engelmoer and Roselaar 1998). ey are mainly distributed in Australia and Southeast Asia during the nonbreeding period and in Far Eastern Russia during the breeding period. Roebuck Bay (RB) in Northwest Australia and Moreton Bay (MB) in East Australia are two major nonbreeding sites for the Whimbrels (Bamford et al. 2008; Rogers et al. 2011; Wilson et al. 2011). Since the 1990s, Whimbrels numbers have declined at MB (Wilson et al. 2011) but increased at RB (Rogers et al. 2019). e causes for these di erent population trends are unclear (Conklin et al. 2014).

Field surveys have revealed seasonal di erences in numbers of Whimbrels at stopover sites along the EAAF. Many birds stopover in the Yellow Sea region during northward migration (Barter 2002; Bamford et al. 2008) but mainly stopover on the coasts of the Kamchatka Peninsula (Gerasimov et al. 2018), south China (Carey et al. 2001; Bai et al. 2015), Indonesia (Eaton et al. 2016) and Papua New Guinea (Bishop 2006) during southward migration (Conklin et al. 2014). However, few surveys were conducted on southward migration (Choi et al. 2016). Shorebird banding and flag resightings (Minton et al. 2006) indicate that the migration route used by the Whimbrels may be more eastward during southward than northward migration, i.e., more birds migrating south use the Kamchatka Peninsula rather than the Yellow Sea region as a stopover site (Minton et al. 2006).

However, not many Whimbrels were flagged and these flagged birds mainly came from nonbreeding sites in East Australia. Moreover, few flagged birds were recovered due to lack of people looking for flags. e annual life cycle of Whimbrels in the EAAF therefore remains unclear.

e rapid development of bio-tracking technology facilitates the identification of the migration routes, key stopover sites, and migration connectivity of migratory birds. In this study, we tracked the nonbreeding Whimbrel populations at MB and RB to identify their breeding sites and stopover sites, and compare their seasonal and population di erences in migration activities. We compare their migration with those of Whimbrels in the East Atlantic Flyway and the Americas Flyway, and we also discuss the potential causes of the di erences in migratory activities.

Methods

Bird capture and tagging

Whimbrels were captured using cannon nets at high tide in MB and RB by the Queensland Wader Study Group (QWSG)/the Australasian Wader Studies Group (AWSG) respectively in the nonbreeding seasons of 2017–2018. ese were part of the banding programs of the Australasian Wader Studies Group (RB) and the Queensland Wader Study Group (MB). At MB, five birds were tagged with 5-g solar Platform Terminal Transmitters (PTTs, Microwave Telemetry, Inc., Columbia, Maryland, US) in November 2017. In February 2018 at RB, five birds were tagged with 5-g PTTs and 11 birds were tagged with 7-g solar Global Positioning System–Global System for Mobile Communication tags (GPS–GSMs, Hunan Global Messenger Technology Co., Ltd., Hunan, China). Tags were attached to the lower back of birds with leg-looped harnesses (Kuang et al. 2019). All of the tagged individuals were adults based on plumage characters (Prater et al. 1977). Relative to the body mass of the individual captured Whimbrels, the tag weight ranged from 1.1 to 2.0%.

e PTT duty cycle was set to 10 h on/48 h o . GPS–GSM tags were programed to make one record of location (fix) at 2–6 h intervals. Only the fixes with high positioning accuracy (error < 500 m for PTTs and < 100 m for GPS–GSM tags) were included in this study.

Data processing

All of the tagged Whimbrels initially remained near the capture site after release. We assumed that the birds had initiated their northward migration when they flew northward more than 50 km from the capture sites and did not return. We assumed that birds had arrived at the breeding site when they no longer moved northward and when two successive fixes were less than 50 km

Data analysis

Of the 21 tagged Whimbrels, eight completed both the northward and southward migration (three from MB and five from RB), and another two from RB completed the northward but not the southward migration. Individuals failed to track were due to equipment failure or death of birds. For example, four birds with tags were resighted in the field but no data received, and one bird was killed in Yakut, Russia by local hunter, and two birds were lost when encountering typhoon in the East China Sea. We analyzed migration data from birds that completed at least a single trip, including 10 birds (7 with PTTs and 3 with GPS–GSMs) that completed northward migration and 8 birds (7 with PTTs and 1 with GPS–GSMs) that completed southward migration. Mantel tests were used to analyze the strength of migration connectivity between the nonbreeding and breeding sites of the two populations (Ambrosini et al. 2009). e pairwise distance matrix for each of the two populations was established based on the geographical location of the nonbreeding and breeding sites for each individual (Ambrosini et al. 2009). e distance matrix included all individuals that arrived at the breeding site during northward migration (seven individuals from RB and three individuals from MB). Distance between individuals was calculated as the great circle distance. e "ADE4" package in R was used to calculate the Mantel correlation coe cient (r_M) for each population (Dray and Dufour 2007). e larger the coe cient, the stronger the migration connectivity.

A two-tailed Welch *t*-test was used to compare the migration activities of the RB and MB population in the same season. We calculated the logarithm of the seasonal ratio of migration speed, overall stopover duration, and travel speed for each individual in order to compare the seasonal di erence in migration activities (Nilsson et al. 2013; Schmaljohann 2018). Linear mixed models (LMMs) were used to analyze the e ect of travel speed and overall stopover duration on the seasonal di erence in migration speed, with individual as a random variable. All statistical analyses were conducted with R software (R Core Team 2018), and results are reported as mean ± SD.

Results

Migration routes and stopover sites

During their northward migration, Whimbrels from the same nonbreeding site followed a similar migration route for their first leg of flights after departure (Fig. 1a, b). e seven tagged birds from RB (Northwest Australia) flew over Southeast Asia to stopover sites on the south China coast, and then moved northward along the coast to the Yellow Sea region (Fig. 1a). e three tagged birds from MB (East Australia) flew over the Western Pacific to stopover sites on the Japan or Yellow Sea coast (Fig. 1b). e first leg flight from RB was 4791 ± 222 km, which represented 44% of the total northward migration distance (11,018 km). e first leg flight from MB was 7121 ± 412 km, which represented 55% of the total northward migration distance (12,991 km). Both the flight distance and duration were significantly longer ($t = 9.23$, df = 2.52 and $p = 0.006$ for flight distance; $t = 2.38$, df = 3.65 and $p = 0.04$ for duration) from MB than from RB (Table 1). e seven birds from RB flew different migration routes after departure from the Yellow Sea region, and their breeding sites were dispersed over a large region in Far Eastern Russia, i.e., from 105.1° to 173.3° E (Fig. 1a). In contrast, the three birds from MB flew a similar migration route and their breeding sites were concentrated in the east of Far Eastern Russia, from 167.7°–172.3° E (Fig. 1b). e migration connectivity (r_M) was 0.39 and 0.99 for birds from RB and MB, respectively.

During southward migration, six of the seven birds from RB followed migration routes that were similar to their northward migration routes and stayed at one or more stopover sites in mainland China; in contrast, one of the seven RB birds, which had a breeding ground at the east of Far Eastern Russia, flew across the Western Pacific to Bismarck Archipelago and then returned to RB (Fig. 1c). Of the three birds from MB, one stopped over in the Yellow Sea, and two flew across the Western Pacific from the Kamchatka Peninsula to Bismarck Archipelago. All three flew back to MB after a stopover at Papua New Guinea (Fig. 1d). e first leg flight of the southward migration was 1292 and 2182 km for birds from MB and RB, respectively; these distances represented about 10% of the total migration distance for each population (Table 1).

None of the tagged birds paused their migration in Southeast Asia during their northward migration. e main stopover sites were located along the coast of China and Northeast Asia. Nine of the 10 tagged birds stopped over in the Yellow Sea region and the other one stopped over in Japan (Fig. 1a, b). During southward migration, most birds from the RB stopped over in the coastal region of China including the Yellow Sea region and Southeast Asia, except for the one RB bird that bred in the east of Far Eastern Russia (Fig. 1c). All three birds from MB, however, stopped over in Kamchatka and eastern Papua New Guinea/Bismarck Archipelago, but only one used the Yellow Sea and none used Southeast Asia as a stopover site (Fig. 1d). Birds stopped over one more time during southward (4.0 ± 1.2 times) than the northward (2.7 ± 1.3 times) migration (two populations combined).

Migration routes of the Whimbrels breeding in the East of Far Eastern Russia were further east and shorter during southward than the northward migration. All four

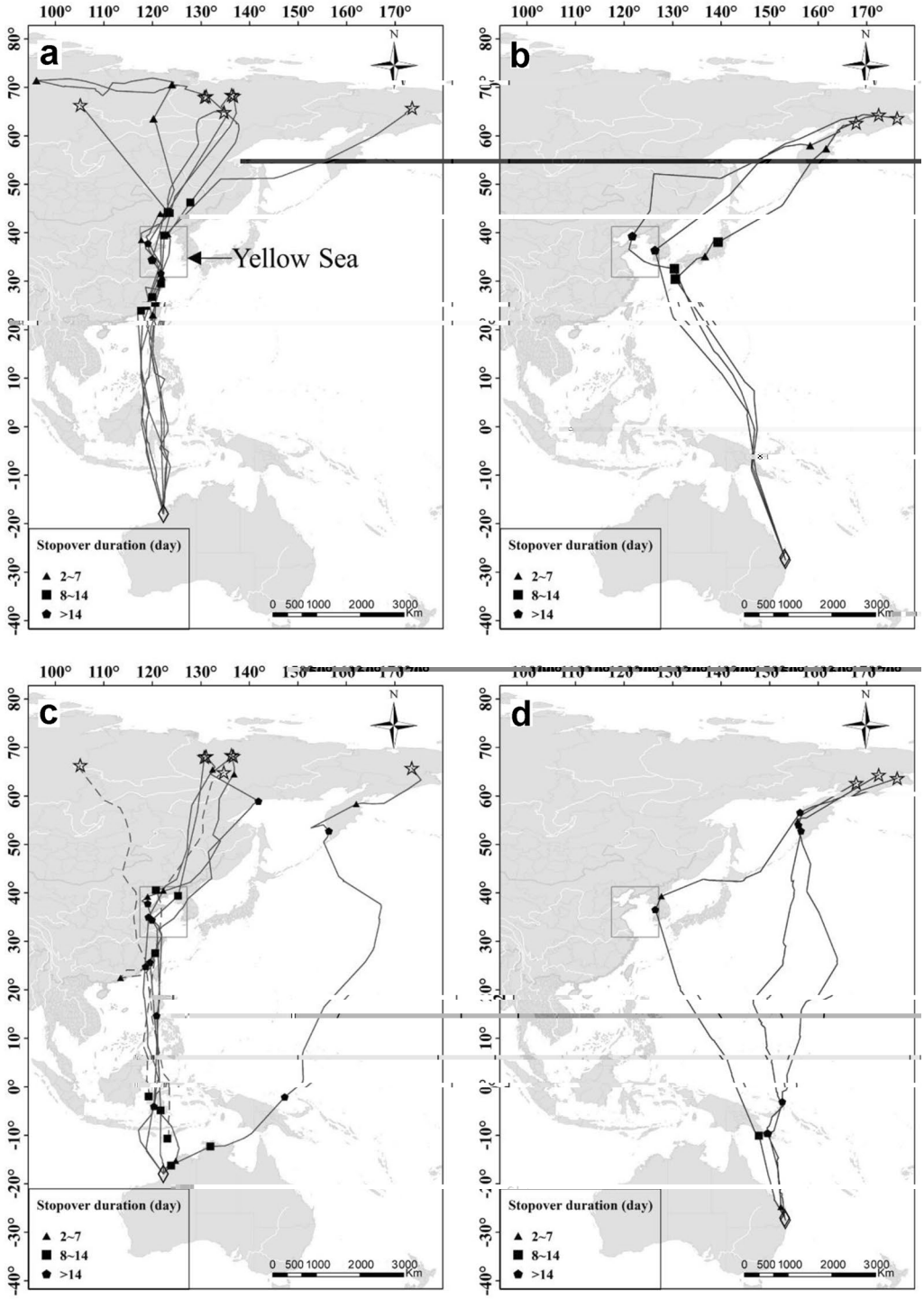

Fig. 1 Nonbreeding sites (diamonds in Australia), northward (**a**, **b**) and southward (**c**, **d**) migration routes, stopover sites (filled in symbols), and breeding sites (pentagrams) of Whimbrels captured at Roebuck Bay (**a**, **c**) and Moreton Bay (**b**, **d**). Solid lines show the complete one-way migration routes, and dotted lines show incomplete one-way migration routes of individual birds

Table 1 Migration parameters of the Whimbrels from Moreton Bay (MB) and Roebuck Bay (RB) in Australia during their northward and southward migration in 2018

Migration characteristics	Northward migration			Southward migration		
	MB ($n=3$)	RB ($n=7$)	Total ($n=10$)	MB ($n=3$)	RB ($n=5$)	Total ($n=8$)
Distance of the first leg flight (km)	7121 (412)	4791 (222)	5490 (1156)	1292 (135)	2182 (1917)	1915 (1624)
Percentage of the first leg flight distance (%)	55 (6)	44 (6)	48 (8)	10 (1)	11 (10)	11 (8)
Duration of first leg flight (days)	6.1 (0.9)	4.6 (0.8)	5.1 (1.1)	1.1 (1.5)	2.3 (1.2)	1.9 (1.3)
Stopover duration in Yellow Sea (days)	14.4 (14.3)	11.6 (9.4)	12.4 (10.3)	11.2 (19.3)	26.1 (23.9)	20.5 (22.2)
Stopover duration in Yellow Sea (%)	50.4 (50.0)	48.3 (38.6)	48.9 (39.4)	17.8 (30.8)	38.2 (38.7)	30.5 (35.2)
Stopover duration in China's coast (days)	5.0 (8.7)	18.3 (4.9)	14.3 (8.6)	0 (0)	28.8 (18.0)	18.0 (20.2)
Stopover duration in China's coast (%)	17.0 (29.4)	77.6 (22.2)	59.4 (37.1)	0 (0)	48.2 (34.4)	30.1 (36.1)
Date of start migration	18-Apr (1.4)	19-Apr (0.9)	19-Apr (1.1)	29-Jul (2.5)	27-Jul (8.1)	28-Jul (6.9)
Date of finish migration	3-Jun (6.5)	28-May (11.3)	30-May (10.0)	22-Oct (8.4)	25-Oct (36.3)	24-Oct (27.8)
Migration distance (km)	12,991 (716)	11,018 (1769)	11,609 (1763)	12,565 (140)	11,418 (969)	11,848 (945)
Migration duration (days)	45 (6)	39 (11)	41 (10.10)	84 (7)	94 (35)	90 (27.4)
Migration speed (km/day)	291 (27)	289 (366)	290 (32.2)	149 (11)	134 (43)	140 (33.9)
Overall stopover duration (days)	29.3 (1.1)	24.2 (4.5)	25.7 (4.5)	66.5 (7.1)	66.4 (31.9)	66.4 (26.2)
Detour index of migration route	0.79 (0.05)	0.89 (0.11)	0.86 (0.11)	0.81 (0.02)	0.86 (0.05)	0.84 (0.04)

(D)

birds used stopover sites in the Yellow Sea and adjacent region (Japan) during their northward migration, but three of the four birds took a shorter migration route, flying across the Western Pacific without a stopover in Asia during their southward migration.

A total of 67 stopover sites used by Whimbrels were identified in this study, including 29 sites during northward migration and 38 sites during southward migration. During northward migration, stopover sites mainly concentrated in the Yellow Sea and the South China while during south migration, stopover sites were dispersed along migration routes including southeast Asian where birds did not stopover during northward migration (Fig. 1, Additional file 1: Table S1).

Migration timing and stopover duration

During northward migration, there was no significant di erence between the two populations in the departure date from nonbreeding sites ($t=1.01$, df$=2.81$, $p=0.39$) or arrival date at breeding sites ($t=0.90$, df$=6.78$, $p=0.40$). e migration distance was nearly 2000 km longer for birds from MB than for birds from RB ($t=2.51$, df$=7.97$, $p=0.04$), but migration duration did not significantly di er between the two populations ($t=1.08$, df$=7.014$, $p=0.32$). e detour index was slightly lower ($t=1.94$, df$=7.68$, $p=0.05$) for birds from MB than for birds from RB. e overall migration speed was similar ($t=0.07$, df$=5.34$, $p=0.94$) between the two populations (Table 1).

During southward migration, the two populations did not significantly di er in the departure date from the breeding sites ($t=0.78$, df$=7.83$ and $p=0.46$) or the arrival date at the nonbreeding sites ($t=0.18$, df$=4.67$ and $p=0.87$) (Table 1). Migration distance was about 1000 km longer for birds from MB than from RB, but migration duration did not significantly di er ($t=0.57$, df$=4.48$, $p=0.60$) between the two populations. e detour index and overall migration speed were similar ($t=1.51$, df$=5.07$, $p=0.19$) for the two populations (Table 1).

During northward migration, the overall stopover duration was longer ($t=2.84$, df$=7.37$, $p=0.01$) for birds from MB than for birds from RB. Two of three birds from MB and six of seven birds from RB stopped over in the Yellow Sea region. Both stopover duration ($t=0.32$, df$=2.78$, $p=0.77$) and percentage of the overall stopover duration ($t=0.06$, df$=3.08$, $p=0.95$) in the Yellow Sea region were similar between the MB and RB birds (Fig. 1, Table 1).

During southward migration, the overall stopover duration was similar ($t=0.63$, df$=4.58$, $p=0.56$) for birds from MB and RB. Four of the seven birds from RB stopped over in the Yellow Sea region for 35.5 ± 16.1 days, which accounted for $52.6\pm29.3\%$ of the overall stopover duration. e other three birds did not stopover in the Yellow Sea region. One of the three birds from MB stopped over in the Yellow Sea region; that bird remained at stopover sites for 33.5 days, which accounted for 53.3% of its overall stopover duration (Fig. 1, Table 1). None of the three MB birds stopped over in the coastal region of China while the

RB birds stopped over for 28.8 ± 18.0 days, accounting for 48.2 ± 34.4% of the overall stopover duration.

Seasonal di□erence in migration activity

e overall migration speed of birds was faster ($t = 9.51$, df = 14.78, $p < 0.001$) during northward migration than during southward migration (Table 1). is was mainly due to the shorter migration duration and stopover duration during northward migration than during southward migration (Additional file 1: Table S2). ere was no significant di erence in migration distance ($t = 0.37$, df = 14.26, $p = 0.72$) or detour index ($t = 0.55$, df = 12.51, $p = 0.59$) between the northward migration and the southward migration (Table 1).

Discussion

is study provided new information on the migration of Whimbrels from two nonbreeding sites (RB and MB) in the EAAF. e dates for the start and end of the migration were similar for the two populations in both seasons, perhaps because the latitudes of breeding sites are similar for the two populations. Migration routes, stopover sites, and stopover duration, however, di ered between the populations and between seasons. Moreover, the migration connectivity between nonbreeding and breeding sites was strong for the MB population (all birds nested in a narrow longitudinal band in Far East Siberia) but weak for the RB population (birds nested across a broad band spanning ~60 degrees of longitude). Seasonal and population di erences in migration highlight the importance of identifying the full annual movements of multiple populations of the same species in the same flyway.

Migration of Whimbrels in the EAAF

Using band recovery and flag resighting data, Minton et al. (2006) suggested that, unlike most shorebirds in the EAAF that pass through the coasts of the Asian mainland during their northward migration, Whimbrels take an eastward migration route and their main stopover sites are located in the Kamchatka region of Far Eastern Russia and Japan. Field surveys also have indicated the importance of Kamchatka for Whimbrels on both northward (Lappo et al. 2012) and southward (Gerasimov et al. 2018) migration. is is consistent with our tracking results for Whimbrels from MB (located in East Australia) but inconsistent with our tracking results for Whimbrels from RB (located in Northwest Australia). It is not surprising because most of the banded and flagged Whimbrels were from East Australia (Minton et al. 2006). In the current study, we found that unlike the Whimbrels from MB, Whimbrels from RB depend on the stopover sites along the coasts of the Asian mainland during both their northward and southward migration. Actually, of the two recovered birds that originate from RB, one was recovered in the south Yellow Sea (Minton et al. 2006). As a consequence, the inconsistence might be due to relatively few birds being flagged in RB and lack of people looking for flagged birds along the coasts of the Asian mainland at the study period (Ma et al. 2013a). Results from our tracking study support speculation by Minton et al. (2006) that "there is only one report from the Yellow Sea in China but… this under-reflects the true importance of the Yellow Sea as a migratory stopover for this species". Moreover, Minton et al. (2006) exhibited that all the breeding region of Whimbrels in Australia is related to Anadyr region in Far Eastern Russia. Our tracking study identified two new breeding regions (central-northern Sakha and eastern Krasnoyarskiy Kray) for Whimbrels in RB. ese breeding regions fit well with the breeding distribution shown by Lappo et al. (2012).

We found that, during their northward migration, the Whimbrels that breed in the east of Far Eastern Russia tend to veer or "detour" westward to the Yellow Sea region (Fig. 1b). is has been found in several species that spend the non-breeding season in eastern Australia or New Zealand, such as the Grey-tailed Tattler (*Tringa brevipes*, Coleman et al. 2018), the Ruddy Turnstone (*Arenaria interpres*, Minton et al. 2011), and the Bar-tailed Godwit (*Limosa lapponica baueri*, Battley et al. 2012). e "detours" may be related to the use of stopover sites in the Yellow Sea region for fuel deposition. Suitable breeding period is short for shorebirds breeding at high latitudes; arriving at breeding sites in good condition is therefore important so that breeding can be quickly initiated. Many studies have indicated that shorebirds in the Yellow Sea region during their northward migration deposit huge amounts of fuel that can be used for both the migratory flight and activities at breeding sites (e.g., Hua et al. 2013; Ma et al. 2013b). During their southward migration, in contrast, birds can restore their body condition after arriving at nonbreeding sites.

Whimbrels from Australia are believed to breed mainly in Far Eastern Russia (Barter 2002; Bamford et al. 2008). However, the migration connectivity between nonbreeding and breeding populations is still unclear. Although sample sizes were small, this study showed that the Whimbrels from MB breed in a relatively small region in the southeast of Chukchi, while the breeding areas of the Whimbrels from RB are more widely distributed in Far Eastern Russia. is indicates that the migration connectivity is stronger for Whimbrels from MB than from RB. All eight individuals that were successfully tracked for their round-trip migration returned to the nonbreeding sites in the previous year, suggesting that Whimbrels exhibit high fidelity to their nonbreeding sites. Further analysis of the genetic traits of birds at various breeding

and nonbreeding sites should help clarify the migration connectivity and gene flow in the flyway.

N. p. variegatus was considered to be the only subspecies in the EAAF with breeding at the east of Far Eastern Russia (Bamford et al. 2008; Conklin et al. 2014). In this study, the breeding grounds of most tracked birds match the breeding range of *variegatus* but new breeding regions (central-northern Sakha and eastern Krasnoyarskiy Kray) were identified for RB birds. ese regions have been suggested to be the overlap zone of subspecies *phaeopus* and *variegatus* (Engelmoer and Roselaar 1998) and the nature of intergradation is unclear. Although our tracking results cannot identify whether there is intergradation between the two subspecies and whether *phaeopus* and *variegatus* might even be di erent species (Livezey 2010), we found RB Whimbrels have a widespread breeding region in Far Eastern Russia. Combining with migratory tracking, comparison on the morphological and genetic traits of birds at both breeding and nonbreeding sites will help to clarify the issue in taxonomy.

We detected obvious seasonal di erence in the use of stopover sites. During northward migration, birds took a long-distance, nonstop flight after departing from nonbreeding sites, and their stopover sites were therefore concentrated in the second half of their migratory journey, i.e., along the coasts of China, Japan, and the Yellow Sea region. During southward migration, stopover sites were widely distributed on the Kamchatka Peninsula, the Yellow Sea region, and the coasts of China, southeast Asia, and Papua New Guinea and the Bismarck Archipelago (Fig. 1c, d). is is consistent with the results from field surveys (Barter 2002; Hadden 2004; Bishop 2006; Bamford et al. 2008; Bai et al. 2015) and reported in McClure (1974). Our tracking results confirm field observations by Gerasimov et al. (2018), for Whimbrels that breed in East Siberia, the Kamchatka Peninsula is an important gathering site during southward migration before their cross-sea southward flight. Our tracking results also indicated that the Kamchatka Peninsula was less used during the northern migration. Field surveys have reported that about 51% (Gerasimov et al. 2018) to 91% (Schuckard et al. 2006) of the Whimbrels in the EAAF stopped over on the Kamchatka Peninsula during southward migration, which is much more than birds recorded during northward migration, although a large number of birds also can be recorded on northward migration (Lappo et al. 2012).

Most of stopover sites the Whimbrels used in this study have been identified as the sites of international importance (Bamford et al. 2008; Conklin et al. 2014) but some new recognized sites have not yet (Additional file 1: Table S1). During northward migration, the newly recognized sites were concentrated in the south coast and the northeast of China, where RB birds did stopover at. During southward migration, the newly recognized sites were concentrated in the southwest coast of Kamchatka, Papua New Guinea and Bismarck Archipelago, south coast of China, and Sulawesi in Indonesia (Additional file 1: Table S1). Although large flocks of Whimbrels have been reported in the southeast Asia on southward migration and nonbreeding period (Conklin et al. 2016), the detailed sites recorded by our tracking are di erent from former records. Field surveys in these regions are required to clarify the importance of these sites for the Whimbrels and other shorebirds.

e first leg of the migratory flight during northward migration is far for both MB and RB populations, i.e., the leg covers about half of the total migration distance. is is also the case for some other shorebirds that spend the nonbreeding period in Oceania and that breed in the Arctic and subarctic (Additional file 1: Table S3). Fuel deposition rate of shorebirds is relatively low at low latitudes where there is less food (macrobenthos on tideland) than at high latitudes (Piersma et al. 2004). To improve their fuel deposition rate, shorebirds can take a long-distance, nonstop flight to "jump over" the low latitudes (Piersma et al. 2004; Aharon-Rotman et al. 2016). is requires high-quality habitats with abundant food to support rapid fuel deposition pre-migration at nonbreeding sites. During their northward migration, birds from MB exhibited longer first leg flights than birds from RB, suggesting that birds from MB deposit more fuel than birds from RB before the onset of migration. is inference is supported by the body mass data at the two sites: there was no significant di erence in body mass between the two populations from October to December; while at pre-migration period in March, body mass of the Whimbrels at MB was significantly higher than that at RB (Additional file 2: Figure S1). We therefore suggest that high quality habitats at nonbreeding sites are important for long-distance migration.

We found RB population intensively used China's coast including the Yellow Sea during both northward and southward migration, while MB population less used during southward migration. is is similar to the migration of Bar-tailed Godwits in the EAAF: *menzbieri* Godwits (mainly stay in Northwest Australia in nonbreeding season) use the Yellow Sea on both migrations while *baueri* Godwits (mainly stay in New Zealand and East Australia in nonbreeding season) use the Yellow Sea only on northward migration (Battley et al. 2012). *Menzbieri* population su ered more rapid decline than *baueri* population; this is likely due to their di erent dependence on the stopover sites in the Yellow Sea, where the critical tidal habitats su ered dramatic loss over the past several decades (Conklin et al. 2016). However, Whimbrel

populations have declined at MB (Wilson et al. 2011) but increased at RB in the recent few decades (Rogers et al. 2019). is is the opposite of the situation of Godwits. is may be because the Whimbrels can use a variety of habitat types (including widely distributed farmland and shrub) during migration (Kuang et al. 2019), thus tidal habitat loss along China's coast had limited impact on the Whimbrels. Recent study indicated that huge numbers of Whimbrels were killed by local hunters in Kamchatka (37,000 birds per year, Khlokov et al. 2020), suggesting MB birds that breed in the east of Far Eastern Russia su ered serious hunting pressure. Further studies on the survival rates at di erent periods and sites in the full annual life cycle (e.g., Piersma et al. 2016) are important to clarify the di erent trends between the two populations.

Migration of Whimbrels in di□erent □yways

Recent studies have indicated that Whimbrels that breed in North America and Iceland use only a limited number of stopover sites during migration. ey generally make one stopover during their northward migration, and Icelandic Whimbrels can fly directly from the breeding to nonbreeding site during their southward migration (Alves et al. 2016; Johnson et al. 2016; Carneiro et al. 2019, Additional file 1: Table S4). Whimbrels in the EAAF, in contrast, stopover for an average of three and four times during their northward and southward migration, respectively. is might be related to the longer migration distances of the Whimbrels in the EAAF (11,000 and 13,000 km for birds from MB and RB, respectively) than in the other two flyways (9800 and 6700 km for birds in North America and Iceland, respectively, Additional file 1: Table S4). Wind conditions (tailwinds or headwinds) in di erent regions can also a ect stopover decisions during migration (Alerstam et al. 2003; Ma et al. 2011; Carneiro et al. 2019). Whimbrels that breed in Iceland and North America are likely to obtain wind assistance (Alves et al. 2016; Johnson et al. 2016; Carneiro et al. 2019) while birds in the EAAF might encounter unfavorable tailwinds near the equator (Wang et al. 2020) and in the south hemisphere during southward migration (Gill et al. 2014). e adverse wind condition can increase the possibility of stopover of birds during migratory flight (Ma et al. 2011).

Because the fuel deposition rate at stopover sites is much slower than the fuel consumption rate during flight, stopover duration is much longer than the duration of migratory flight, and thus migration speed is mainly determined by stopover duration (Kölzsch et al. 2016; Schmaljohann 2018). In the EAAF, Whimbrels have shorter stopover durations and thus faster migration speeds during their northward than their southward migration. is is consistent with results obtained for most migratory birds and is related to the time pressure for early arrival at breeding sties during northward migration (Newton 2008; Nilsson et al. 2013). Whimbrels that breed in Iceland and North America, however, have a shorter stopover duration and thus a faster migration speed during their southward than northward migration (Alves et al. 2016; Johnson et al. 2016; Carneiro et al. 2019, Additional file 1: Table S4). It is likely that Whimbrels that breed in Iceland and North America have a greater chance of obtaining tailwind assistance during their southward than northward migration. is benefits the migratory flights from breeding to nonbreeding sites (Alves et al. 2016; Johnson et al. 2016; Carneiro et al. 2019). e relatively short migration distance of Whimbrels breeding in Iceland also enables those birds to make a nonstop flight from the breeding to the nonbreeding site.

In response to the narrow breeding time window at high latitudes, some birds adopt a capital breeding strategy, i.e., they deposit nutrients that form the eggs before arriving at breeding sites (Hobson and Jehl 2010) and can therefore lay eggs soon after arriving at breeding sites. Capital breeders generally have a relatively long stopover duration en route (especially at final prebreeding stopover sites), which enables them to deposit more fuel than required for the migratory flight (Hua et al. 2013). Whimbrels that breed in North America at least partially adopt a capital breeding strategy (Hobson and Jehl 2010). ey spend 64 days at the breeding site and 34 days at stopover sites during their northward migration, and there is only an 11-day interval between arriving at the breeding site and laying eggs (Johnson et al. 2016). In contrast, Whimbrels that breed in Iceland tend to be income breeders (Carneiro et al. 2019). ey have a short stopover duration during their northward migration (12 days), remain for a long period at the breeding site (95 days), and exhibit a long interval between arriving at the breeding site and laying eggs (22 days) (Carneiro et al. 2019). e current study indicates that Whimbrels in the EAAF have an average stopover duration of 26 days during northward migration and remain at the breeding site for 59 days (Table 1, Additional file 1: Table S4), which is similar to the Whimbrels in North America. As a consequence, we speculate that Whimbrels in the EAAF at least partially adopt a capital breeding strategy and that the conservation of key stopover sites that enable fuel deposition en route is critical for their population maintenance.

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