RESEARCH

Seasonal and regional differences in migration patterns and conservation status of Swan Geese (*Anser cygnoides*) in the East Asian Flyway

Iderbat Damba[1,2,3†], Junjian Zhang[1†], Kunpeng Yi[1], Huashan Dou[4], Nyambayar Batbayar[5], Tseveenmyadag Natsagdorj[5], Batmunkh Davaasuren[5], Lei Cao[1,2*] and Anthony David Fox[6]

Abstract

Background: The Swan Goose (*Anser cygnoides*) breeds across Mongolia and adjacent China and Russia and winters exclusively in China. It is globally threatened, showing long-term major range contractions and declining abundance, linked to habitat loss and degradation. We remain ignorant about the biogeographical subpopulation structure of the species and potential differences in their migration timing, stopovers and schedules, information that could be vital to effective conservation of different elements of the species population, which we address here with results from a telemetry study.

Methods: In 2017–2018, we attached GPS/GSM telemetry devices to 238 Swan Geese on moulting sites in three discrete parts of their summering area (Dauria International Protected Area, Central Mongolia and Western Mongolia), generating 104 complete spring and autumn migration episodes to compare migration speed and nature between birds of different summer provenances.

Results: Birds from all three breeding areas used almost completely separate migration routes to winter sympatrically in the Yangtze River floodplain. Although many features of the spring and autumn migrations of the three groups were similar, despite the significantly longer migration routes taken by Western Mongolian tagged birds, birds from Dauria Region arrived significantly later in winter due to prolonged staging in coastal areas and took longer to reach their breeding areas in spring. Among birds of all breeding provenances, spring migration was approximately twice as fast as autumn migration. Areas used by staging Swan Geese (mainly wetlands) in autumn and spring almost never fell within national level protected areas, suggesting major site safeguard is necessary to protect these critical areas.

Conclusions: This study showed the discreteness of migration routes taken by birds of different summer provenances and differences in their migratory patterns, highlighting key staging areas (Yalu River Estuary in China/North Korea for Dauria Region breeding birds, Daihai Lake for Central Mongolian and Ordos Basin for Western Mongolian birds). Based on this new knowledge of the biogeographical subpopulation structure of the Swan Goose, we need to

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*Correspondence: leicao@rcees.ac.cn

†Iderbat Damba and Junjian Zhang: Shared first authors

[1] State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100085, China

Full list of author information is available at the end of the article

combine data on subpopulation size, their distribution throughout the annual life cycle and conservation status, to develop more effective conservation strategies and measures to reverse population decline throughout the range.

Keywords: *Anser cygnoides*, GPS/GSM telemetry, Migration parameters, Segmentation, Stopover duration, Swan Geese

Background

The Swan Geese (*Anser cygnoides)* is an endemic East Asian species listed by IUCN as Vulnerable, which now breeds mainly in Mongolia and adjacent areas of Russia and China and migrates to winter almost exclusively in China (Batbayar et al. 2011; An et al. 2018; Damba et al. 2020). The species has shown long-term major contractions of breeding and wintering range as well as recent continued declines in abundance (Fox and Leafloor 2018; Damba et al. 2020). These are thought to be linked to habitat loss and degradation due to human activities through climate change, agriculture, aquaculture and urbanization, as well as the direct effects of hunting (Gombobaatar and Monks 2011; BirdLife International 2018; Chen et al. 2019). Survival rates of neck-collared telemetry tagged Swan Geese revealed low autumn survival rates, especially among juveniles (Choi et al. 2016), but we still remain ignorant about the biogeographical subpopulation structure of the species and potential differences in their migration timing, stopovers and schedules, information that could be vital to effective conservation of different elements of the species population.

In this study, we report, compare and contrast the findings from telemetry results from Swan Geese fitted with GPS/GSM transmitter collars marked in three different core breeding areas in Mongolian plateau. In particular, we wished to compare and contrast (1) migration routes, (2) migration parameters and (3) stopover sites used by Swan Geese from the three breeding areas in autumn and spring to contribute and improve the efforts for their effective conservation.

Methods

Tracking geese marked with GPS/GSM transmitters

Swan Geese breed across all of Mongolia, but are most concentrated into three core areas by the availability of wetlands, separated by arid landscapes with more restricted nesting habitat. In this study, we attempted to mark birds from each of these three discrete areas to compare their migration patterns and levels of protection. In Western Mongolia, Swan Geese breed in large lakes located in the semi-desert region of the Great Lakes Depression, where the annual temperature range is highest and it is significantly warmer and drier during the breeding season. Swan Geese breeding in Central Mongolia nest on lakes and along rivers located in the short

grass steppe biome set among middle elevation rolling hills, where annual precipitation is higher than the other capture regions. Swan Geese in the Dauria region, in Eastern Mongolia, breed in lakes and river valleys located on more flat steppe areas generally surrounded by tall grass steppe habitat, which experiences the mildest climate compared to the other two areas (Batchuluun and Dash 2020). There are estimated 600 moulting Swan Geese at Aireg Lake and Uws Lake, which are the major breeding areas in Western Mongolia; estimated 3000 moulting birds at Ugii Lake, which is the largest moulting concentration in Central Mongolia; estimated 25,000 moulting birds in the Dauria region and Eastern Mongolia (Fox and Leafloor 2018). The capture areas were 700–1000 km separate from each other (Fig. 1).

In three different parts of the breeding area, flightless moulting Swan Geese were captured by herding them up using boats and kayaks and pushing them onto land into funnel drive-traps (Bub 1991). In Western Mongolia, two geese were marked with 35 g GPS/GSM transmitters manufactured by Druid Technology, China at Uws Lake (50.4° N, 93.1° E) in July 2017, three marked with 44 g transmitters manufactured by Ornitela, UAB at Uws Lake and eight with 44 g Ornitela transmitters at Taigan Lake (46.4° N, 97.4° E) in July 2018. In Central Mongolia, 25 geese were marked with 35 g Druid transmitters at Ugii Lake (47.8° N, 102.7° E) in July 2017. In Dauria International Protected Area (47.7° N, 117.5° E), 200 geese were marked with 35 g Druid transmitters in July 2017. All these GPS/GSM transmitters were neck collar-mounted and constituted less than 1.2% to Swan Geese body mass to minimize the impact on their behaviour and ecology (Millspaugh and Marzluff 2001; Bodey et al. 2018). Devices attached in 2017 and 2018 were set to record the GPS locations at 1 h and 10 min intervals, respectively, throughout the research project. Bench tests prior to deployment confirmed the horizontal accuracy of transmitters as 9.6 m (SD = ± 5.6 m).

Data from tracked geese contributed 104 completed autumn and spring migration episodes (Additional file 1: Table S1). To avoid pseudo-replication, only the first autumn and spring migration tracks were selected from each individual.
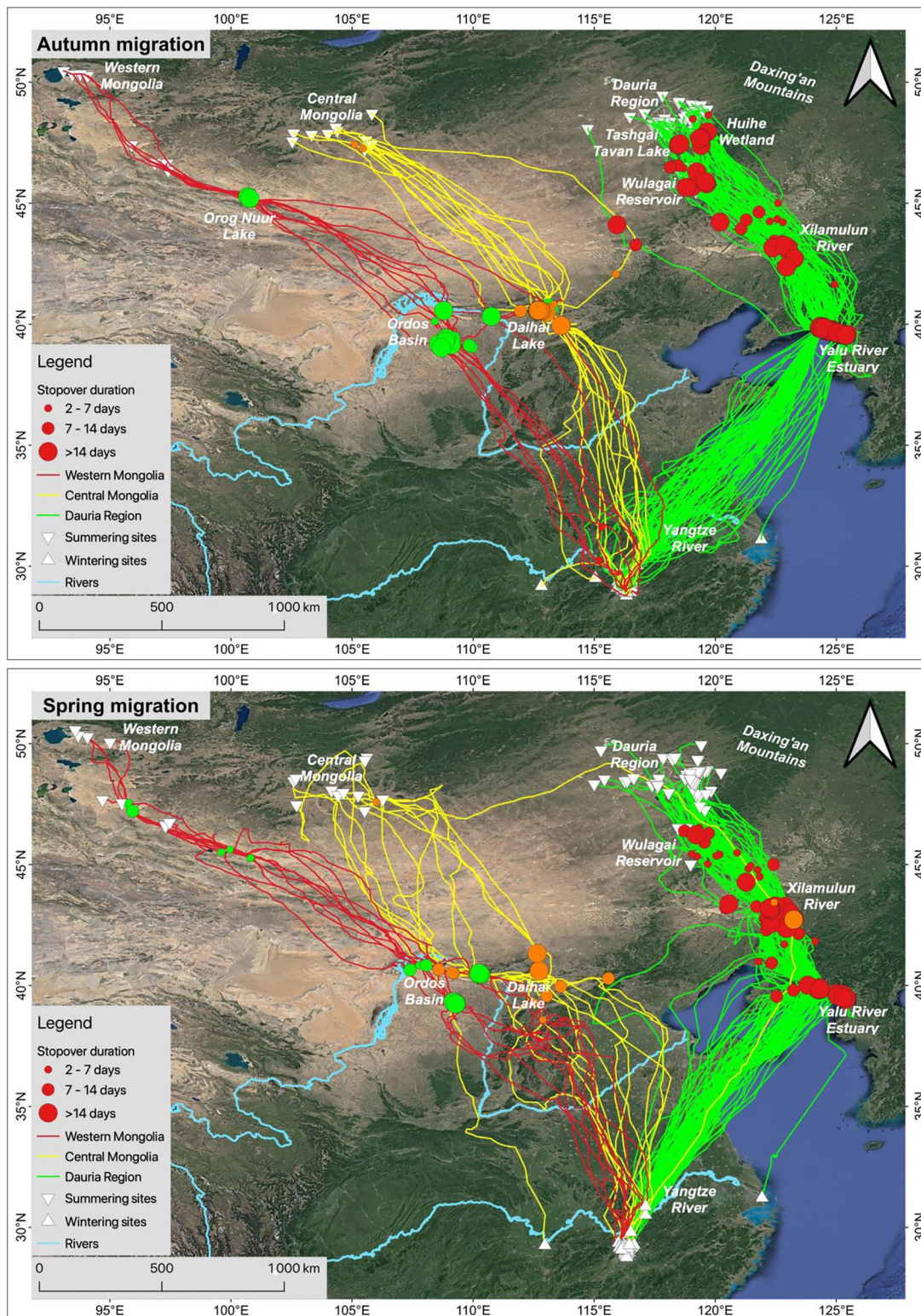
Fig. 1 Autumn and spring migration routes and stopover sites of Swan Geese (*Anser cygnoides*) marked with GPS/GSM telemetry in three breeding sites. The green lines and red circles show the migration routes and stopover sites of geese in Dauria Region; the yellow lines and orange circles, Central Mongolia; the red lines and green circles, Western Mongolia. The size range of points represents the stopover duration of 2–7 days, 7–14 days and > 14 days, respectively. White inverted triangles represent the breeding sites, white regular triangles represent the wintering sites

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Identifying stopover sites

We applied the method of Wang et al. (2018b) to segment movement tracks into periods of "flight" and "non-flight". A cluster of positions within a radius of 35 km and within a period of 48 h was defined as a stopover site (48 h defined as the minimal time required to rest and start accumulating energy stores from feeding; Drent et al. 2006; Kölzsch et al. 2016). If subsequent tracking positions from an individual fell outside of this radius, but the same individual returned to the same stopover site again subsequently, then those points were still determined to be in the same stopover cluster (van Wijk et al. 2012).

Land-use and conservation status of stopovers

To characterize the landcover and assess the effectiveness of the current extent of designated protected areas for the protection of stopover sites used by tracked geese, we only retained the GPS locations where the velocity between adjacent points was less than 1 km/h to exclude the fast-moving positional fixes during stopovers (Zhang et al. 2020). In order to compare between the land-use and conservation status of stopovers in different migration routes, we divided these stopover sites into different geographical regions based on mountain ranges, river basins and country boundaries, such as the Daxing'an Mountains (a.k.a Greater Khingan Mountain) and Yellow River (Fig. 1, Table 2).

To characterize the landcover at stopover sites, we used the Land Cover Atlas of the People's Republic of China (resolution 30 m × 30 m; Wu et al. 2017) for GPS locations within China, and the "FROM-GLC 2017v1" land cover dataset (resolution 10 m × 10 m) created by the Department of Earth System Science, Tsinghua University (Gong et al. 2019) for GPS locations outside of China. We divided landcover types into several broad categories, namely wetland, grassland, cropland, bare substrate (including bare soil, desert and salina) and others (including forest and artificial surface) (Gong et al. 2013). We assigned each GPS location within the stopover sites to a specific land-use type defined by the land cover data using R 3.6.0 (R Core Team 2019).

To assess the conservation status at stopover sites, we downloaded the boundary information from the National Nature Reserves of China (http://www.resdc.cn/data.aspx?DATAID=272), Database of Mongolian Protected Areas (Ministry of Nature, Environment and Tourism, Mongolia) and World Database of Protected Areas (WDPA 2018; accessed at protectedplanet.net) for North Korea. We then overlaid stopover sites within QGIS 3.18 to identify which GPS fixes were located within protected area boundaries in different countries.

Defining migration parameters

We defined the departure date as the time and date of the position when the individual departed from summering/wintering sites and was judged by the methods above to have an acquired "flight" status. Arrival date was defined as the first time when the individual was judged to have arrived at wintering/summering sites, based on the methods above to qualify as "non-flight" status after a period of "flight". Migration duration was calculated as the time the individual took to migrate (including stopovers) between the last summering and first wintering position (autumn migration) or between the last wintering and the first summering position (spring migration). A site where an individual bird spent more than two days resting and feeding during migration was defined as stopover site (Kölzsch et al. 2016) and the number of stopovers was calculated accordingly. The stopover duration was derived as the sum of all days spent at all stopover sites. Thus, the days actually spent traveling (total travel days) was calculated as total migration duration minus stopover duration. We defined flight leg as the journey connecting subsequent stopover, wintering or summering sites, to generate the number of flight legs involved in each autumn/spring episode. We defined migration distance as the cumulative travel distance between summering and wintering sites. Step length was calculated as the migration distance divided by the number of flight legs during each migration season. We calculated the path tortuosity of the movement between summering and wintering areas in both directions using the straightness index (Benhamou 2004). Based on the above results, we were able to calculate migration speed as migration distance divided by migration duration, and the travel speed was calculated by dividing migration distance by total travel days (Wang et al. 2018a; Deng et al. 2019).

Comparison of migration parameters

For the spring and autumn migration parameters, we used paired student *t*-tests to test for significant differences between seasons among birds tagged at each of the three different breeding areas. We used ANOVA tests and Tukey–Kramer tests for statistical differences between the three groups of geese from the different breeding areas. All the analyses were conducted within R. All data presented in the tables and text in the form of estimated means ± SD unless otherwise stated.

Results

After rejection of repeats (to avoid pseudo-replication), we obtained a total of 104 Swan Geese which finished both complete autumn and spring migration episodes during 2017–2019, including 81 birds captured at Dauria Region, 13 birds at Central Mongolia and 10 birds Western Mongolia. Although all of these geese wintered in the Yangtze floodplain, they selected different migration routes during autumn and spring migration to travel there (Fig. 1).

Geese from Dauria Region

Geese summering in Dauria Region started autumn migration between 28 August and 29 September (median date = 12 September, $N = 81$). Two birds started in late August, and the other 79 geese started in September. Geese arrived on the Yangtze River wintering sites between 17 October and 8 December (median = 18 November). Of these, 13 birds arrived at their wintering grounds in late October, 50 birds arrived in November, and 18 birds arrived in early December. Geese took on an average of 64.1 ± 15.4 days to complete their 2677.9 ± 159.7 km southbound migration. Autumn stopover sites used by geese were concentrated between Dauria Region (summering site) and Yalu River Estuary, but any stopovers were rarely used between the Yalu River and Yangtze River (see Fig. 1).

Geese started their spring migration from the wintering grounds between 4 and 26 March (median = 21 March) and selected the Yalu River Estuary as their first goal for staging stopovers. The first birds arrived at the summering grounds on 9 April and the last one arrived on 1 May (median = 16 April). Most of the birds arrived at the breeding grounds in April but a single bird arrived at the beginning of May. Geese spent 29.7 ± 6.2 days to complete 2710.4 ± 221 km northbound migration. The few spring stopover sites were located between the Yangtze River and Yalu River Estuary, and most of them concentrated between the Yalu River Estuary and the Huihe Wetland (see Fig. 1).

Although the routes and distance taken by the Dauria Region Swan Geese were similar, there were significant differences in migration patterns between two migration seasons (Table 1 and Figs. 2 and 3). The migration duration of spring migration was 34 days, significantly shorter than autumn migration (df = 80, $t = 19.0$, $P < 0.001$). Swan Geese flew during spring migration twice as fast as in autumn (95.1 km/day for spring migration and 44.9 km/day for autumn migration, df = 80, $t = -19.1$, $P < 0.001$). The travelling duration in spring was 0.62 days longer than autumn migration (df = 80, $t = -2.93$, $P < 0.01$). The travel speed in

spring (averaged 735 km/day) was significantly slower than autumn (averaged 857.6 km/day; df = 80, $t = 3.31$, $P < 0.001$). The stopover duration in spring migration was 34 days, significantly shorter than that during autumn migration (df = 80, $t = -19.83$, $P < 0.001$), while the number of stopover sites did not differ significantly between the seasons (df = 80, $t = -1.6$, $P = 0.117$). The step length did not differ significantly between the two seasons (df = 80, $t = -1.9$, $P = 0.06$).

Geese from Central Mongolia

Geese summering in Central Mongolia started autumn migration between 3 and 28 September (median = 13 September, $N = 13$) and arrived at the wintering ground between 24 October and 23 November (median date = 31 October). Six birds arrived at their wintering grounds in the end of October and seven birds arrived in November. Geese took an average of 53.7 ± 9 days to complete the 2603.8 ± 166.3 km southbound migration. During autumn migration, all of the tagged birds used just one area located near Daihai Lake as stopover site (see Fig. 1).

Geese started spring migration from the wintering grounds between 9 and 21 March (median = 21 March). The first birds arrived at the breeding grounds on 24 March and the last one arrived on 20 April (median = 5 April). Four birds arrived at the breeding grounds and in March and the other nine arrived in April. Geese spent 20.8 ± 8.1 days to complete the 2927.8 ± 388.8 km northbound migration. During migration, most of geese selected Daihai Lake and Ordos Basin as their stopover sites. In addition, one bird chose the same spring migration route as that used by geese from Dauria Region initially and flew back from Eastern Mongolia (see Fig. 1).

Although the autumn and spring migration routes and distance taken by Central Mongolia Swan Geese were similar, there were significant differences in migration patterns (Table 1, Figs. 2 and 3). The migration duration of spring migration was 32 days significantly shorter than in autumn (df = 12, $t = 8.5$, $P < 0.001$). The travel speed in spring (averaged 685.8 km/day) is slower than autumn (averaged 891.4 km/day; df = 80, $t = 3.31$, $P < 0.001$). Swan Geese daily flew 3 times faster during spring than autumn migration, which averaged 159.8 km/day in spring and 50 km/day in autumn and stopover duration in spring migration was 34 days, shorter than that in autumn migration (df = 12, $t = 9.2$, $P < 0.001$). Numbers of stopover sites averaged 1.6 during spring migration compared to 1.9 during autumn, which did not differ significantly.

Geese from Western Mongolia

Geese summering in Western Mongolia started autumn migration between 15 August and 4 October

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Table 1 Mean values (± SD) and *t*-tests comparing the migration parameters of tracked Swan Geese during spring and autumn migration in the three different migration routes
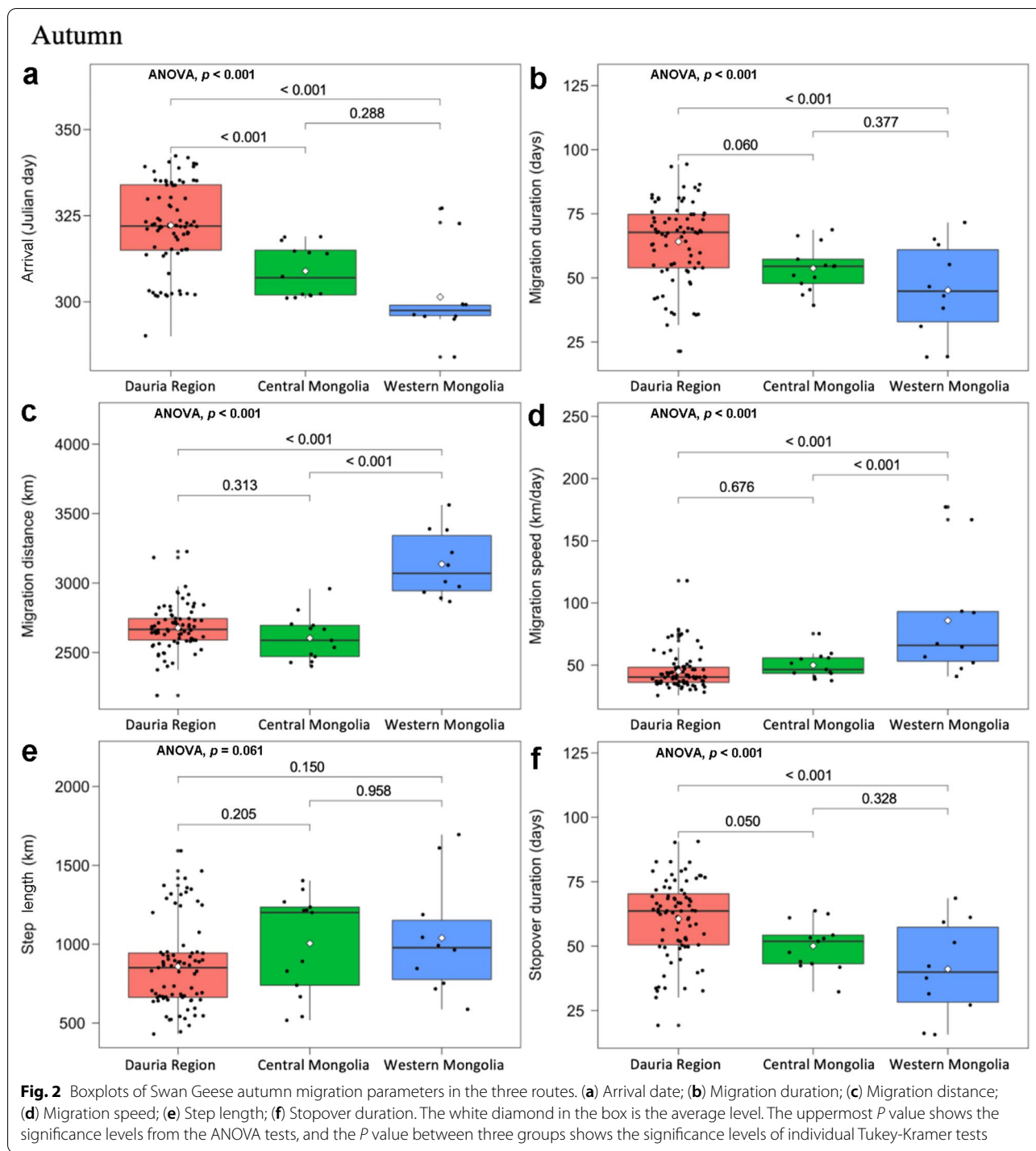
Routes	Parameter	Mean value ± SD		df	*t*	*P* value
		Spring	Autumn			
Dauria Region (*N* = 81)	Departure (Julian date)	75.9 ± 5.8	257.9 ± 7.3			
	Arrival (Julian date)	105.9 ± 4.1	322.2 ± 12.2			
	Migration duration (day)	29.7 ± 6.2	64.1 ± 15.4	80	19.0	< 0.001
	Migration distance (km)	2710.4 ± 221.0	2677.9 ± 159.7	80	− 1.2	0.216
	Migration speed (km/day)	95.1 ± 20.3	44.9 ± 14.7	80	− 19.1	< 0.001
	Number of stopover sites	2.6 ± 0.9	2.4 ± 1.0	80	− 1.6	0.117
	Stopover duration (day)	25.7 ± 5.9	60.6 ± 15.1	80	19.8	< 0.001
	Travel duration (day)	3.8 ± 1.1	3.2 ± 1.4	80	− 2.9	0.004
	Travel speed (km/day)	735 ± 196.5	857.6 ± 250.3	80	3.3	0.001
	Step length (km)	793.5 ± 200.6	858.6 ± 271.4	80	1.9	0.064
	Straightness index	0.8 ± 0.0	0.8 ± 0.0	80	− 0.1	0.937
Central Mongolia (*N* = 13)	Departure (Julian date)	74.8 ± 5.8	255 ± 8.0			
	Arrival (Julian date)	95.8 ± 8.7	308.9 ± 7.6			
	Migration duration (day)	20.8 ± 8.1	53.7 ± 9.0	12	8.5	< 0.001
	Migration distance (km)	2927.8 ± 388.8	2603.8 ± 166.3	12	− 2.8	0.016
	Migration speed (km/day)	159.8 ± 56.1	50 ± 10.5	12	− 6.6	< 0.001
	Number of stopover sites	1.6 ± 0.7	1.9 ± 1.2	12	0.9	0.393
	Stopover duration (day)	16.1 ± 7.4	50.1 ± 9.3	12	9.2	< 0.001
	Travel duration (day)	4.6 ± 1.4	3.5 ± 1.9	12	− 1.7	0.114
	Travel speed (km/day)	685.8 ± 224.1	891.4 ± 406.6	12	1.5	0.162
	Step length (km)	1169.3 ± 249.2	1005.4 ± 317.1	12	− 1.8	0.098
	Straightness index	0.8 ± 0.1	0.9 ± 0.0	12	2.6	0.024
Western Mongolia (*N* = 10)	Departure (Julian date)	72.6 ± 4.0	256.1 ± 14.7			
	Arrival (Julian date)	98.5 ± 5.2	301.4 ± 13.2			
	Migration duration (day)	25.6 ± 5.3	45.2 ± 18.6	9	3.2	< 0.05
	Migration distance (km)	3341.1 ± 284.9	3136.1 ± 242.4	9	− 2.4	< 0.05
	Migration speed (km/day)	136 ± 30.3	85.8 ± 48.7	9	− 2.9	< 0.05
	Number of stopover sites	1.8 ± 0.4	2.3 ± 0.9	9	1.5	0.177
	Stopover duration (day)	19.5 ± 5.4	41.1 ± 18.8	9	3.6	< 0.01
	Travel duration (day)	6.1 ± 1.5	4.1 ± 1.1	9	− 3.3	< 0.05
	Travel speed (km/day)	572.8 ± 130.3	801.1 ± 177.0	9	3.1	< 0.05
	Step length (km)	1224.7 ± 251.8	1039.3 ± 367.3	9	− 1.3	0.213
	Straightness index	0.8 ± 0.1	0.9 ± 0.0	9	2.0	0.078

(median = 10 September, *N* = 10). One bird started migration in the middle of August, seven in the September and two in the beginning of October. Geese arrived at the wintering grounds between 11 October and 19 November (median = 24 October). Eight birds arrived in the end of October and the other two arrived in November. During southbound migration, geese spent an average of 45.2 ± 18.6 days completing 3136.1 ± 242.4 km migration. All birds used stopover sites in the Ordos Basin.

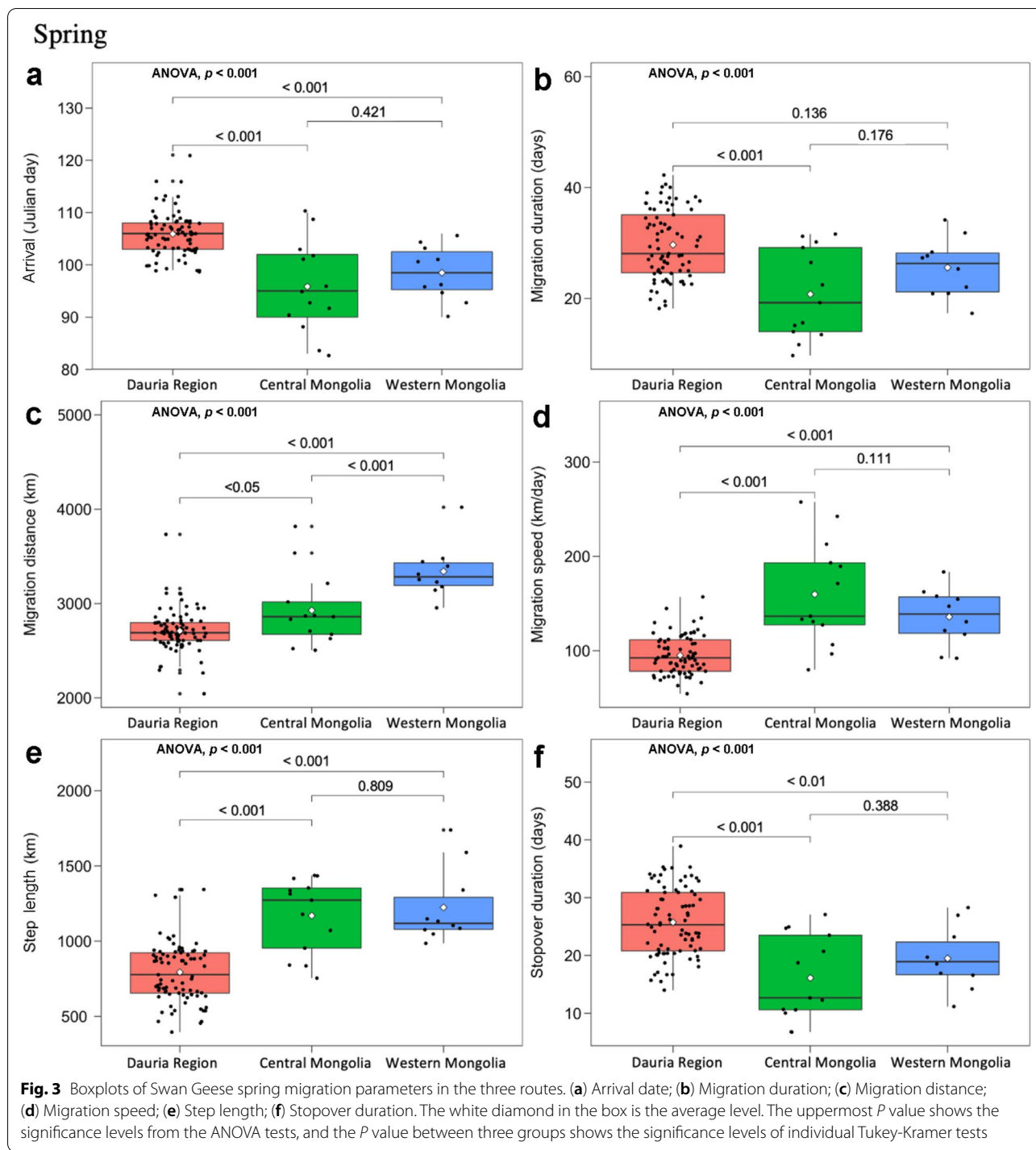Geese started spring migration from the wintering grounds between 6 and 21 March (median = 8 March), and arrived at their summering grounds between 11 and 25 April (median = 20 April). Geese spent 25.6 ± 5.3 days completing 3341.1 ± 284.9 km northbound migration. Most of geese selected the Ordos Basin, as the first stopover for a prolonged rest, followed by shorter periods at their second stopover in Mongolia.

Although migration routes and distances taken by Western Mongolia Swan Geese were similar, there were again significant differences in migration patterns (Table 1 and Figs. 2 and 3). The duration of spring migration was 25.6 days, significantly shorter than in autumn (df = 9, *t* = 3.2, *P* < 0.05). The mean migration

Fig. 2 Boxplots of Swan Geese autumn migration parameters in the three routes. (**a**) Arrival date; (**b**) Migration duration; (**c**) Migration distance; (**d**) Migration speed; (**e**) Step length; (**f**) Stopover duration. The white diamond in the box is the average level. The uppermost *P* value shows the significance levels from the ANOVA tests, and the *P* value between three groups shows the significance levels of individual Tukey-Kramer tests

speed of spring migration was 136 km/day compared to 85.8 km/day in autumn, which means Swan Geese flew faster during spring migration than autumn migration (df = 9, $t = -2.9$, $P < 0.05$). The travel duration in spring was 2 days longer than autumn migration (df = 9, $t = -3.3$, $P < 0.05$). The travel speed on

spring migration was significant slower than that of autumn migration (averaged 572.8 km/day in spring and 801.1 km/day in autumn; df = 9, $t = 3.1$, $P < 0.05$). The stopover duration in spring migration was 25 days less than that during autumn migration (df = 9, $t = 3.6$, $P < 0.01$), while the numbers of stopover sites did not

Fig. 3 Boxplots of Swan Geese spring migration parameters in the three routes. (**a**) Arrival date; (**b**) Migration duration; (**c**) Migration distance; (**d**) Migration speed; (**e**) Step length; (**f**) Stopover duration. The white diamond in the box is the average level. The uppermost *P* value shows the significance levels from the ANOVA tests, and the *P* value between three groups shows the significance levels of individual Tukey-Kramer tests

differ significantly between the seasons (df = 9, $t = 1.5$, $P = 0.177$).

Comparison of the three migration routes

During autumn migration, the migration distance taken by geese from Western Mongolia was longer than those migrating from Dauria Region and Central Mongolia (adj.$P < 0.001$; ANOVA: $F_{2,101} = 35.58$, $P < 0.001$). Although geese from all three summering areas started migration on similar dates ($F_{2,101} = 0.83$, $P = 0.438$), geese from Dauria Region arrived significantly later at the Yangtze River than geese from Western and Central

Mongolia (adj.$P < 0.001$; $F_{2,101} = 39.06$, $P < 0.001$). This was the result of longer migration duration (adj.$P < 0.001$; adj.$P = 0.06$; $F_{2,101} = 8.70$, $P < 0.001$) and stopover duration (adj.$P < 0.001$; adj.$P = 0.05$; $F_{2,101} = 9.48$, $P < 0.001$). The migration speed of geese from Western Mongolia was faster than those from Central Mongolia and Dauria Region (adj.$P < 0.001$; $F_{2,101} = 18.89$, $P < 0.001$).

ANOVA tests showed the same significant differences in spring as in autumn for departure date, arrival date, migration distance, migration duration and stopover duration. The migration speed of geese from Dauria Region was slower than among those from Western and Central Mongolia (adj.$P < 0.001$; $F_{2,101} = 35.98$, $P < 0.001$). The geese from Dauria Region used more stopover sites than geese from Western and Central Mongolia (adj.$P = 0.01$; adj.$P < 0.001$; $F_{2,101} = 11.47$, $P < 0.001$), which resulted in significantly shorter step lengths (adj.$P < 0.001$; $F_{2,101} = 32.08$, $P < 0.001$).

The major stopover regions

Tracking identified eight major stopover regions used by the Swan Geese during autumn and spring migration (see Fig. 1 for locations). Among these, the Yalu River Estuary was the most important for geese from Dauria Region during both autumn and spring migration. Daihai Lake was important for geese from Central Mongolia during autumn migration, while the Ordos Basin was important for geese from Central Mongolia during spring migration and geese from Western Mongolia during both autumn and spring migration periods (Table 2).

(1) Huihe Wetland, Inner Mongolia, China: 14 geese used this site for an average of 13.7 days in autumn. These small, sandy lakes are located near a known bird catching area, around 150 km away. The land-use of stopover sites located here included 64% wetland, 22% cropland and 12% grassland in autumn (Fig. 4). The percentage of positions used by staging birds was only 3.5% (Table 2).

(2) Tashgai Tavan Lake, Dornod Province, Mongolia: Six geese used this lake as a stopover site during autumn migration for an average of 15.9 days. The land-use of stopover sites located here included 67% wetland, 22% grassland and 10% bare substrate in autumn. This region is not protected.

(3) Wulagai Reservoir, Inner Mongolia, China: 20 geese stayed for an average of 12.8 days in autumn, 11 geese (6.5 days) in spring. The land-use of stopover sites located here included 67% wetland, 12% bare substrate and 10% grassland in autumn, 69% wetland and 28% grassland in spring. This region is not protected.

(4) Xilamulun River, Inner Mongolia and Liaoning Province, China: 25 geese stayed for a mean of 16.8 days (autumn) and 71 geese for 13.1 days (spring) at many small lakes in a sandy landscape, where they fed on nearby rice fields and roosted on lakes. The land-use of stopover sites located here included 68% wetland and 24% grassland in autumn, 56% wetland and 35% cropland in spring. The percentage of the areas used by geese that is protected was only 4.3% in autumn and 1.2% in spring.

(5) Yalu River Estuary China/North Korean border: geese staged here for 9–80 days (mean = 48.8, $N = 78$) in autumn and 2–29 days (mean = 14.7, $N = 65$) in spring, feeding and roosting in the intertidal estuary and mud flats. The land-use of stopover sites located here included 94% wetland in autumn, 83% wetland and 14% cropland in spring. This area used by the geese during these periods is almost totally un-protected.

(6) Daihai Lake, Inner Mongolia and Shanxi Province, China: Central Mongolian Swan Geese mainly rested here, on average remaining 50.1 days in autumn. Only four geese (average duration 16.2 days) rested here in spring. All geese in this area fed and roosted near lakes. The land-use of stopover sites located here included 78% wetland and 12% grassland in autumn, 68% wetland, 20% grassland and 11% cropland in spring. This region is not protected.

(7) Orog Nuur Lake, Bayanhongor Province, Mongolia: Western Mongolian Swan Geese mainly rested here as the first stopover sites during autumn migration (average duration 10.9 days). The land-use of stopover sites located here included 55% wetland, 29% bare substrate and 15% grassland in autumn. This region is not protected.

(8) Ordos Basin, Inner Mongolia, China: In autumn, Western Mongolian Swan Geese mostly stayed in the middle of basin (average stay 33.0 days), used 34% grassland, 30% bare substrate, 15% cropland and 14% others. In spring, both Central and Western Mongolian Swan Geese stayed at stopover sites close to the Yellow River (average 11.0 and 16.2 days respectively), used 70% cropland and 10% grassland. Only 3.9% (autumn) and none of the areas used in spring by staging birds are currently protected.
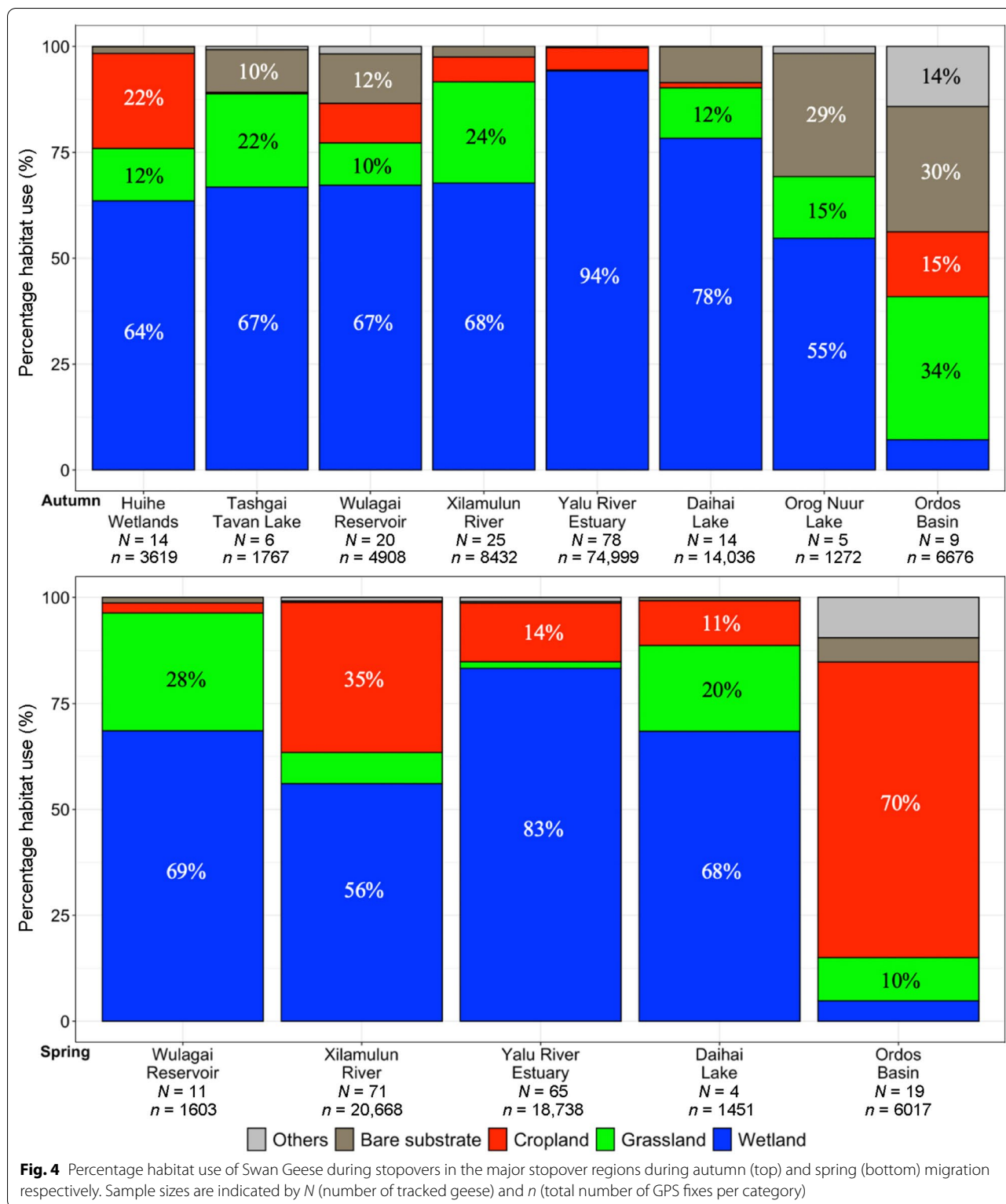
Discussion

We used data from 104 Swan Geese tracked using GPS/GSM telemetry to identify the spring and autumn migration parameters, migration route and stopover sites

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Table 2 Major stopover regions used by tracked Swan Geese during spring and autumn migration

Capture location	ID	Country	Name	Season	No. of birds	Bird days	Average days	Date range	Range in days	Protection percentage at national level (%)
Dauria Region	1	China	Huihe Wetland (47.77° N, 119.42° E), Inner Mongolia	Autumn	14	192	13.68	8/29–9/27	4–25	3.48
	2	Mongolia	Tashgai Tavan Lake (47.42° N, 118.50° E), Dornod Province	Autumn	6	95	15.87	9/7–10/9	10–22	0.00
	3	China	Wulagai Reservoir (46.04° N, 119.38° E), Inner Mongolia	Autumn	20	255	12.75	9/6–10/10	3–23	0.00
				Spring	11	71	6.45	4/1–4/30	2–20	0.00
	4	China	Xilamulun River (43.43° N, 122.60° E), Inner Mongolia/Liaoning Province	Autumn	25	420	16.79	8/29–11/17	2–58	4.33
				Spring	71	908	13.13	3/16–4/19	3–28	1.18
	5	China/ North Korea	Yalu River Estuary (39.71° N, 124.81° E), Liaoning Province/North Pyongan Province	Autumn	78	3,808	48.82	9/12–12/7	9–80	0.01
				Spring	65	953	14.66	3/6–4/16	2–29	0.03
Central Mongolia	6	China	Daihai Lake (40.46°N, 113.01°E), Inner Mongolia/Shanxi Province	Autumn	13	642	50.11	9/5–11/18	30–61	0.00
				Spring	4	65	16.20	3/11–4/18	7–27	0.00
	7	China	Ordos Basin (40.50° N, 109.81° E), Inner Mongolia	Spring	9	99	11.00	3/11–4/8	7–17	0.00
Western Mongolia	8	Mongolia	Orog Nuur Lake (45.15° N, 100.80° E), Bayanhongor Province	Autumn	5	54	10.87	8/15–9/26	3–26	0.00
	9	China	Ordos Basin (39.72° N, 109.22° E), Inner Mongolia	Autumn	9	297	33.02	9/11–11/21	16–55	3.88
				Spring	10	162	16.19	3/12–4/7	6–25	0.00

Only sites selected by at least four birds and where the estimated duration of stay was at least 2 days are shown

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Fig. 4 Percentage habitat use of Swan Geese during stopovers in the major stopover regions during autumn (top) and spring (bottom) migration respectively. Sample sizes are indicated by *N* (number of tracked geese) and *n* (total number of GPS fixes per category)

from birds using three different breeding areas. For the first time, these data were able to show that, despite following three discrete migration routes, Swan Geese all came to winter together in one place, the Yangtze River floodplain. Despite the fact that the birds tagged in Western Mongolia undertook significantly longer migration

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routes, those birds recorded faster travel speeds, with the result that they and the birds tagged in Central Mongolia arrived earliest to wintering areas, significantly earlier than birds tagged at Dauria Region, which generally had the shortest migration distances. This was because Dauria Region birds spent significantly longer at their stopover sites than birds from either of the other two breeding areas. Dauria Region and Central Mongolian birds generally departed their summering areas and subsequent stopover sites in autumn when local temperatures approached or fell below freezing (unpubl. data), supporting the frost hypothesis of Xu and Si (2019). On the return migration, Dauria Region birds arrived significantly later to the breeding areas than either Central or Western Mongolian birds, again the result of spending longer periods on the stopover sites en route. Arrival of tagged Swan Geese from the Dauria Region and Central Mongolian breeding areas to their stopover sites coincided with minimum temperatures exceeding freezing point (unpubl. data), suggesting the extent of frost was determining their movement northwards in spring as well. This may suggest that the rate of movement along their flyways was determined by the annual rate of spring thaw and that this could contribute to the observed differences between the three groups following different spring migration routes, but more tracking data from multiple seasons are needed to confirm this.

Despite the sympatric nature of their wintering grounds, tagged Swan Geese showed almost discrete migration corridors back to their respective breeding areas, as had been the case during autumn migration (Fig. 1). As a result, birds from the different breeding provenances used largely mutually exclusive staging stopover sites along their respective migration corridors. In autumn, Swan Geese tagged at Dauria Region mostly used the Yalu River Estuary, Central Mongolian birds used Daihai Lake heavily in autumn (but also by some individuals in spring) and Western Mongolian Swan Geese used the Ordos Basin staging areas (in autumn and spring). Interestingly, nine Central Mongolian tagged birds also used the Ordos Basin as a spring staging stopover site. Away from Ordos Basin, > 55% of positions used by autumn staging Swan Geese (and > 56% spring) were in wetlands. The remainder were mainly on grassland and cropland dependent upon agriculture. While this implies that the extent, availability and quality of these natural habitats are adequate to support these birds with overspill to agricultural land, the future safeguard of these wetlands requires protection as local and national nature reserves. In the Ordos Basin, autumn geese used a variety of different habitats which perhaps suggests problems finding adequate food during that season, but were heavily reliant on cropland in spring, suggesting in comparison with the other staging areas, this area has insufficient wetland resources available to these birds during the critical spring migration and prelude to breeding. Furthermore, a superficial comparison between tracking positions and protected area site boundaries suggests that birds from all three summering areas use autumn and spring staging areas that enjoy almost no nature conservation protection at national level at all. There is a particular urgent need for autumn stopover sites associated with Daihai Lake and the Ordos Basin to be better protected under local and national nature conservation criteria. We remain lamentably ignorant about the numbers of birds using these areas, food resources and the nature of the safe roosting habitats used by these birds during their stay there. We would therefore urge local studies to determine the most heavily used areas (and therefore most important areas for the geese) as a basis for implementing site safeguard through designation of protected areas. Foraging and ecological studies would also help to improve local habitat management (for instance to provide protection from disturbance and maybe sacrificial crops in areas where geese are heavily dependent upon cropland and farmland) to provide optimal conditions for the birds during the relatively short time they are present in this area. Finally, we would advocate subsequent feedback monitoring to assess the effects of protected area designation and habitat management in relation to subpopulation annual growth rate to protect these areas and the geese using them more effectively in the future.

For the tagged Swan Geese from Dauria Region, Yalu River Estuary was the most important stopover site. The Yalu Estuary is long recognised as a very important spring and autumn staging area for Swan Geese breeding in northeastern Mongolia (Batbayar et al. 2011; Choi et al. 2016), but it is clearly also vital for Inner Mongolian breeding birds from China. Sixty-five of the tagged individuals among the 81 tracked geese (80%) used it as stopover in spring, and 78 individuals (96%) in autumn. Those geese using the site showed the longest average stopover durations there on the Yalu River (49 days in autumn and 15 days in spring, significantly longer than on the Xilamulun River and the Inner Mongolia grassland further north). Indeed, Swan Geese left the Xilamulun River southwards when the daily minimum temperature in autumn was still high (3.7 °C, unpublished data), suggesting more attractive conditions on the Yalu River, which being on the coast with a very extensive intertidal zone enjoys a milder climate, freezing later and thawing earlier than more continental areas at the same latitude. The Yalu Estuary is situated within highly militarised areas, which may give the birds and their habitats some de facto protection, but this is by no means guaranteed.

We therefore also urge more cross border collaboration to encourage joint research programmes, scientific monitoring and international conservation actions to protect these birds during their two important and major staging periods at this vital site.

Our results again confirm among birds tracked from all three migratory corridors, that unlike many Arctic breeding goose species in the same region (e.g. Deng et al. 2019), Swan Geese undertake spring migration faster than in autumn. For all territory holding migratory breeding birds, theory suggests that the earliest arriving birds in the best condition have the greatest chance of securing best territories, breeding earliest and enjoying the longest breeding season (Milonoff et al. 1998; Kokko 1999; Moore et al. 2005). Earlier hatched and fledged young also have greater chance of surviving to breed (Perrins 1970), so there is an imperative for breeding birds to return earliest to their breeding areas, which means spring migration is often of shorter duration than autumn. This has been confirmed among other species, e.g. waders (Alves et al. 2016), gulls (Bustnes et al. 2013), swifts (Henningsson et al. 2009) and songbirds (DeLuca et al. 2015) as well as in Bar-headed Geese (*Anser indicus*) (Hawkes et al. 2013).

The main difference in timing between Swan Goose migrations in the two seasons concerned stopover duration. Migration distance did not differ significantly between spring and autumn for the Swan Goose, but geese took half the time in spring to cover the same distance. In spring, they undertook relatively few migration flight legs, when individual step length was longer than in autumn. Swan Geese stayed much longer at autumn stopover sites than in spring, since overall travel speed was similar.

Conclusions

Use of modern telemetry devices enabled us to identify significant differences in migration duration, speed and stopover duration of Swan Geese tagged in three different parts of the breeding range, which used almost discrete migration routes to sympatric wintering areas in the Yangtze River floodplain. These novel findings suggest the possibility for some degree of population structuring, if individuals using these different migration routes are isolated, as long as genetic continuity is not maintained by pairing on the wintering grounds (as seems likely).

Southbound autumn migration duration and stopover duration of birds tagged at Dauria Region exceeded those marked in Central and Western Mongolia. The autumn migration speed of Western Mongolian Swan Geese was faster than other two routes. However, as all Swan Geese seemed to respond to frost by travelling southwards from breeding and staging areas in the same way,

it seems more likely that the timing of migration along the different migration routes was response to environmental conditions rather than having any basis in genetics or cultural tradition. During spring migration, Central and Western Mongolian birds arrived earlier than Dauria Region birds to the breeding grounds, again seemingly following the vernal thaw.

The most important spring and autumn stopover site for Dauria Region tagged Swan Geese was the Yalu River Estuary during spring and autumn migration. Results showed that tagged birds from Central Mongolian were heavily reliant on Daihai Lake and Western Mongolian birds on the Ordos Basin, drawing attention to the need to adequately protect these stopover sites and ensure the sympathetic management of habitats for the geese during their short, but highly significant stopovers at these sites.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40657-021-00308-y.

Additional file 1: Table S1. Summary table of Swan Geese (*Anser cygnoides*) fitted with solar-powered GPS/GSM telemetry devices.

Declarations

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Author details
[1] State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100085, China. [2] University of Chinese Academy of Sciences, Beijing 100049, China. [3] Institute of Biology, Mongolian Academy of Sciences, Ulaanbaatar 13330, Mongolia. [4] Hulun Lake National Nature Reserve Administration, Inner Mongolia 021008, China. [5] Wildlife Sciences and Conservation Center of Mongolia, Union Building, B-701, UNESCO Str., Ulaanbaatar 14210, Mongolia. [6] Department of Ecoscience, Aarhus University, Aarhus, Denmark.

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