Migration patterns and conservation status of Asian Great Bustard (Otis tarda dybowskii) in northeast Asia

Article *in* Journal of Ornithology · November 2022

DOI: 10.1007/s10336-022-02030-y

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Journal of Ornithology
https://doi.org/10.1007/s10336-022-02030-y

ORIGINAL ARTICLE

Migration patterns and conservation status of Asian Great Bustard (*Otis tarda dybowskii*) in northeast Asia

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Received: 26 June 2022 / Accepted: 17 October 2022

Abstract

The Great Bustard (*Otis tarda*) holds the distinction of the heaviest bird to undertake migration as well as the greatest degree of sexual size dimorphism among living birds. Though the migration of the species has been widely discussed in the literature, researchers know little about the migration patterns of the subspecies in Asia (*Otis tarda dybowskii*), especially the males. In 2018 and 2019, we captured six *O. t. dybowskii* (five males and one female) at their breeding sites in eastern Mongolia and tagged them with GPS-GSM satellite transmitters. This constitutes the first time that the Great Bustards of the eastern subspecies have been tracked in eastern Mongolia. We found sex differences in migration patterns: males started migration later but arrived earlier than the female in the spring; males had 1/3 of the migration duration and migrated about 1/2 the distance of the female. Additionally, Great Bustards exhibited high fidelity to their breeding, post-breeding, and wintering sites. For conservation, only 22.51% of GPS location fixes of bustards were within protected areas, and less than 5.0% for wintering sites and during migration. Within two years, half of the Great Bustards we tracked died at their wintering sites or during migration. We recommend establishing more protected areas at wintering sites and rerouting or undergrounding powerlines in areas where Great Bustards are densely distributed to eliminate collisions.

Keywords Great Bustard · *Otis tarda dybowskii* · Migration · Satellite tracking

Zuammenfassung

Zugmuster und Schutzstatus der Asiatischen Großtrappe (*Otis tarda dybowskii*) in Nordostasien.

Die Großtrappe (*Otis tarda*) ist der schwerste Zugvogel und weist in der Körpergröße den größten Geschlechtsdimorphismus unter den heutzutage lebenden Vögeln auf. Zwar wird der Zug dieser Art in der Literatur ausführlich diskutiert, aber man weiß nur wenig über die Zugmuster der Unterart in Asien (*Otis tarda dybowskii*), vor allem der Männchen. 2018 und 2019 fingen wir sechs *O. t. dybowskii* (fünf Männchen und ein Weibchen) an ihren Brutplätzen in der östlichen Mongolei und versahen sie mit GPS-GSM-Satellitensendern. Dies war das erste Mal, dass die Großtrappen der östlichen Unterart in der östlichen Mongolei nachverfolgt wurden. Wir stellten geschlechtsspezifische Unterschiede in den Zugmustern fest: Männchen begannen ihre Wanderung später, kamen aber früher als die Weibchen im Frühjahr an; Männchen zogen ein Drittel der Zugzeit und

Communicated by N. Chernetsov.

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legten etwa die Hälfte der Strecke der Weibchen zurück. Außerdem zeigten die Großtrappen eine große Standorttreue zu ihren Brut-, Aufzucht- und Überwinterungsgebieten. Zum Schutz der Trappen wurden innerhalb von Schutzgebieten nur 22,51% der GPS-Ortungen vorgenommen und in den Winterquartieren und während des Zugs weniger als 5,0%. Die Hälfte der von uns nachverfolgten Großtrappen starb innerhalb von zwei Jahren in ihren Überwinterungsgebieten oder auf dem Zug. Wir empfehlen, in den Überwinterungsgebieten mehr Schutzgebiete einzurichten und Stromleitungen in Gebieten, in denen Großtrappen stark vertreten sind, umzuleiten oder unterirdisch zu verlegen, um Kollisionen zu vermeiden.

Introduction

The Great Bustard (*Otis tarda*) is one of the heaviest migratory bird species and is listed as Vulnerable (VU) by the International Union for Conservation of Nature Criteria (IUCN 2017). The estimated world population of this globally threatened species is 31,000–36,000 individuals, which was 34% less than 16 years ago (Alonso and Palacín 2022; Alonso 2014). There are two subspecies: the western subspecies (*O. t. tarda*) spread widely in Europe with some small and isolated populations in central Asia (IUCN 2017; Kessler and Smith 2014), with a total estimated population size of 29,243 to 33,372 individuals (Alonso and Palacín 2022); the eastern subspecies (*O. t. dybowskii*), which mainly breeds in Asian Russia, Mongolia, and China, winters almost entirely in China (Collar et al. 2017), and has an estimated population of only 1450–2030 individuals (Alonso and Palacín 2022). The species has a great degree of sexual dimorphism: male Great Bustards weigh 2.4 times more than females (Alonso et al. 2009b), which may be caused by the intense mating competition that occurs within the Great Bustard's dispersed lek mating system (Morales et al. 2003). Both sexes exhibit high fidelity to their habitats (Palacín et al. 2009; Kessler 2015).

The eastern subspecies has fewer individuals and has suffered a long-term decline (Liu et al. 2017) because of human disturbances, including pollution, hunting, and habitat fragmentation (Mi et al. 2016; Mi et al. 2017). Unfortunately, conservation efforts face challenges due to a lack of basic information on their life cycle and ecology. In Europe, the migration patterns of the western subspecies have been widely studied for decades. For example, as partial migrants, the proportion of migratory males was higher than that of females (Palacín et al. 2009) and males migrate longer distance than females (Morales et al. 2000). However, there has only been one migration study of the eastern subspecies, and it tracked the movement of three females (Kessler et al. 2013). It is unclear whether the eastern subspecies has sex differences in migratory patterns as does the western subspecies.

From 2018 to 2019, we tracked 5 males and 1 female *O. t. dybowskii*. This constitutes the first time that Great Bustards of the eastern subspecies have been tracked in eastern Mongolia. The purpose of this study is: (1) to identify the migratory routes and patterns of *O. t. dybowskii*; (2) to determine if and how the sexes differ in migration patterns of *O. t. dybowskii* in northeast Asia; (3) to identify the protected area status of stopover sites and breeding and wintering grounds to provide protection advice for this endangered subspecies.

Methods

Satellite tracking

In June 2018 and 2019, six adult Great Bustards (five males and one female) were safely captured in Ugtam Nature Reserve in Bayandun and Dashbalbar soums in Dornod province in northeastern Mongolia (113.8° E, 49.4° N). After determining the exact location of the Great Bustards based on night vision and thermal imaging at midnight, we turned on the flashlight to cause them visual impairment and captured them with a powerful handheld net (1.5 m long, 1.2 m deep). Considering females may be egg-laying during this period, we only caught one non-breeding female. Bustards were fitted with backpack solar-powered GPS-GSM satellite transmitters (model HQBG3621S, Hunan Global Messenger Technology Company).

Transmitters weigh 24 g with the harness made of carbon fibre, corresponding to 0.13–0.57% of the bustards' body mass. They were released in less than 15 min. We observed tagged bustards for 5 min until they walked away. They were displayed normally in the lek sites the next morning, and no damage was observed. Tracking data were transmitted through the Global System for Mobile Communication (GSM) hourly or every two hours, giving information about the birds' latitude and longitude, instantaneous speed, course, and altitude, along with additional data on the air temperature, battery voltage, and measurement precision.

Data processing

We obtained data on at least one full migration for all six Great Bustards, including 15 seasonal routes from three males (three autumns and two spring migration routes for each bird from autumn 2018 to autumn 2020), two autumn migration routes (in 2018 and 2019) from two males and four migration routes of one female (autumn 2018 to spring 2020). In total, we collected 93,095 location readings (Fig. 1). Each data point was classed into

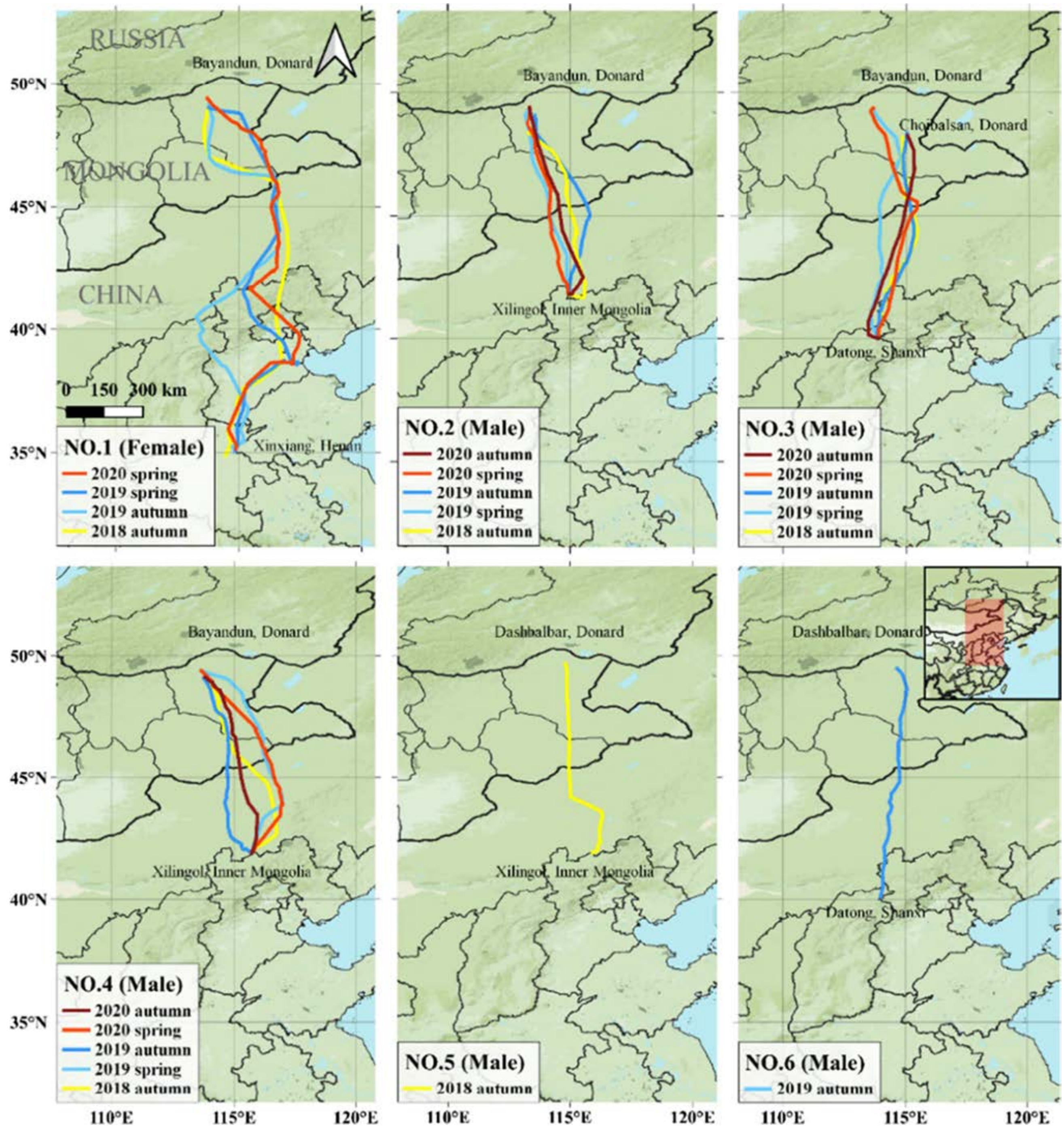


Fig. 1 Migration routes of six Asian Great Bustard individuals tracked using GPS backpacks in northeastern China and eastern Mongolia between autumn 2018 and autumn 2020

one of five levels, A (within 5 m accuracy), B (5–10 m), C (10–20 m), D (20–100 m) and invalid. We only preserved A, B, and C in this study to exclude possibly inaccurate readings.

Migration date and duration

We defined the start of migration as an unreversed movement of at least 40 km in 24 h beginning in their breeding ground or wintering range for the autumn and spring migrations with visual inspection, respectively, and determined the end date of migration as the day of arrival at either the wintering and breeding range for autumn and spring migrations (Gu et al. 2021). We calculated the migration duration for each route by subtracting the start date of migration from the end date of the migration.

Stopovers

We defined stopovers as events between the start and end of their migration where birds moved less than 20 km in 24 h and showed non-directional movements (McCabe et al. 2020; Limiñana et al. 2012). We recorded the duration of each of these events as the stopover duration. We summed the duration of each stopover for each migration route by each individual to obtain a total stopover duration. We divided stopovers into 'short' and 'long' stopovers (McCabe et al. 2020), and used a threshold of 10 days to distinguish the two categories following the convention of Lang (2021). Routes and stopover sites were plotted in QGIS 3.18.1, by distinguishing locations where the flight speed equals zero (Wang et al. 2020).

Migration distance

To calculate migration distance, we retained just one point from each stopover that a bird took to remove redundant points. We obtained a final step length using the 'amt' package (Signer et al. 2019) in R 3.6.3. Then, we summed up all step lengths between the migration start and end dates. We also extracted if a fix was taken during day or night using time_of_day function in amt package to explore whether the Great bustards we tracked migrated at night. We removed points that the step length was less than 10 km and moved less than 20 km in 24 h. Then, we calculated the numbers of movement points and the sum of the migratory distance at night per route. We also visually counted the number of days occupied by each night migration. If the migration lasted from the previous night to the early morning of the next day, it was recorded as one day.

Movement speeds

We calculated the total speed of migration (km/day) by taking an individual's total migration distance (km) and dividing it by total migration duration (days). We calculated the mean flight speed for each migratory route by extracting all data points where the instantaneous speed of the bird was over 10 km/h (Mi et al. 2018). Travel speed (km/day) was calculated as total migration distance divided by the difference between total migration duration and total stopover duration (Schmaljohann 2018).

Site fidelity

We selected the four individuals that were tracked for two full years (from winter 2018 to summer 2020) and calculated the overlaps of a single individual for multiple years that occurred during non-migration seasons. We resampled the data, drawing one point for every 12 h to reduce the spatial auto-correlation and used the data to define home ranges based on 95% KDE (kernel density estimate). Then, we calculated the volumetric intersection between the spatial distributions of each individual's wintering and breeding/post-breeding home range distributions (Fieberg and Kochanny 2005) in the 'amt' package.

Conservation gap analysis

Conservation gap analysis is an efficient method to examine a species's characteristics and management needs (Scott et al. 1993). We obtained nature reserves data from the World Database on Protected Areas (WDPA) (UNEP-WCMC and IUCN 2021) and combined it with data from the Mongolian Ministry of Environment and Tourism (MET; https://eic.mn/geodata/index.php) to assure the accuracy and completeness of the map. We obtained conservation gaps by calculating the number of stop points (flight speed less than 10 km/h) in protected areas (Mi et al. 2018) at wintering sites, breeding/post-breeding sites, and during migration across the study duration.

Data from three females from central Mongolia

As we tracked only one female, we added in previously published data from females tracked in central Mongolia (Kessler et al. 2013) to provide robust evidence on sex differences of eastern subspecies. All females were breeding in Mongolia and wintering in China. Although the accuracy of tracking data and the number of valid GPS points from Kessler et al. (2013) were lower than ours, we considered these minor differences do not affect the analysis results. We used the total duration and migratory distance of three females (Kessler et al. 2013). For data that were in a range, we took the mean value for statistical analysis.

Statistical analysis

We calculated the migratory date, total duration, migratory distance and movement speeds of our tracking data (5 males and 1 female) in R 3.6.3 (Team 2021). We then combined our data with that from the 3 females in central Mongolia (Kessler et al. 2013) and used Mann–Whitney *U* tests to compare sex differences in migratory duration and distance at the subspecies level. We randomly selected one of the migration routes for each individual to avoid pseudo-replication. The data are reported as mean ± SD.

Results

Arrival and departure dates for individuals tracked in the eastern flyway

On average, male Great Bustards started their spring migration on 25 March ± 5.71 days from the wintering sites and arrived at the breeding sites on 7 April ± 6.36 days (Fig. 1; Table 1). The only female started spring migration on 24 February ± 3.54 days and arrived at the breeding site on 26 April ± 7.78 days (Fig. 1; Table 1). In autumn, males began their migration on 7 October ± 13.29 days, which was similar to the female's departure on 8 October ± 0.71 days. The males arrived at their wintering sites on 24 October ± 11.18 days (Fig. 2; Table 1), while females arrived later, on 11 November ± 16.97 days (Fig. 2; Table 1).

Migration duration and distance

Male bustards spent 16.44 ± 14.68 days on migration. The female travelled 47.52 ± 20.04 days on average, which was three times longer than males. Males travelled 945.13 ± 79.00 km, which was half as long as the 1882.63 ± 61.80 km travelled by the female. The difference in migration distance by sex was statistically significant if data from female Great Bustards using a different migratory pathway, 1000 km to the west, are added to the dataset (SI, Tab. S2). Males showed no differences in migration duration and distance between spring and autumn migrations, but females spent twice the amount of time undergoing migration in spring compared to the autumn (Fig. 3; SI, Tab. S1).

Six Asian Great Bustards migrated at night occasionally, and the nocturnal activity increased as dawn approaches (Fig. 4). Averagely, males moved at night for 3.29 ± 1.69 days per migration, with a total distance of 186.39 ± 124.16 km. The single female moved 358.72 ± 212.20 km at night in 6.75 ± 4.43 days per route. The Great Bustards we tracked rarely migrated overnight and usually do not last longer than 3 h. But we found Great Bustard NO.3 moved 333.92 km within 7 h from 21:00 on October 10th, 2019, accounting for 35% of the total migration distance. And individual NO.4 migrated 218.41 km at midnight on 20 October 2020.

Table 1 Summary of migration data of Asian Great Bustards breeding in northeastern Mongolia

Bird	Body mass (kg)	Year	Season	Start date	End date	Duration (days)	Number of stopovers	Distance (km)
NO.1 (Female)	4.20	2018	Autumn	8 Oct	30 Oct	22.13	2 (1 long stopover)	1801.61
		2019	Spring	27 Feb	21 Apr	52.67	2 (2 long stopovers)	1876.49
			Autumn	9 Oct	23 Nov	44.83	7 (1 long stopover)	1949.19
		2020	Spring	22 Feb	2 May	70.46	3 (2 long stopovers)	1903.22
NO.2 (Male)	10.84	2018	Autumn	11 Sep	30 Oct	49.08	2 (0 long stopovers)	853.62
		2019	Spring	3 Apr	8 Apr	5.13	0	960.77
			Autumn	19 Oct	25 Oct	6.04	2 (0 long stopovers)	900.69
		2020	Spring	24 Mar	31 Mar	7.04	1 (0 long stopovers)	874.66
			Autumn	21 Oct	24 Oct	3.96	0	886.38
NO.3 (Male)	10.21	2018	Autumn	17 Oct	27 Oct	10.17	1 (0 long stopovers)	956.14
		2019	Spring	27 Mar	2 Apr	6.21	2 (0 long stopovers)	1073.20
			Autumn	13 Oct	16 Oct	3.04	0	955.92
		2020	Spring	28 Mar	5 Apr	8.17	1 (0 long stopovers)	1088.10
			Autumn	21 Oct	24 Oct	3.04	0	961.09
NO.4 (Male)	11.36	2018	Autumn	21 Sep	24 Oct	33.17	3 (1 long stopover)	911.63
		2019	Spring	18 Mar	15 Apr	28.00	2 (1 long stopover)	955.37
			Autumn	6 Oct	14 Oct	7.75	0	863.16
		2020	Spring	20 Mar	15 Apr	25.96	2 (1 long stopover)	933.91
			Autumn	28 Sep	13 Oct	15.13	3 (0 long stopovers)	840.89
NO.5 (Male)	10.98	2018	Autumn	1 Oct	26 Oct	25.29	2 (0 long stopovers)	949.98
NO.6 (Male)	17.80	2019	Autumn	13 Oct	24 Nov	42.33	4 (2 long stopovers)	1101.77

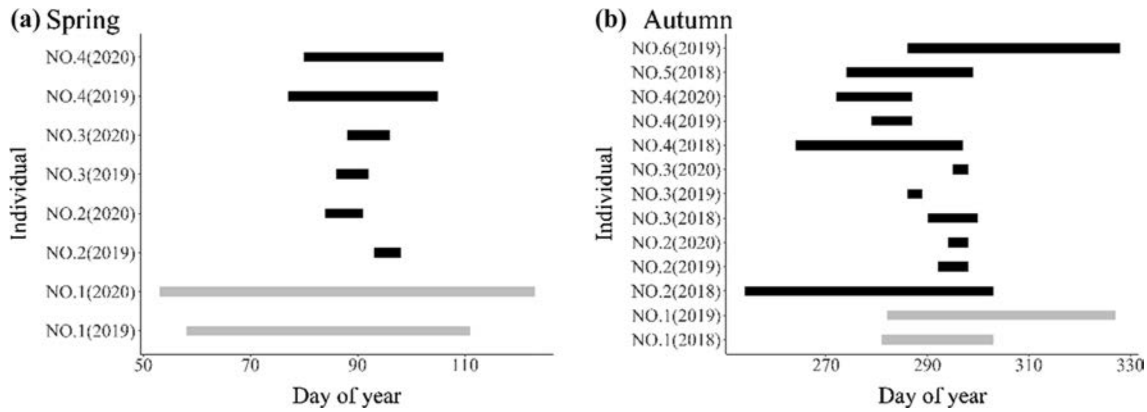


Fig. 2 Migration dates of Great Bustards breeding in northeastern Mongolia for each **a** spring and **b** autumn migration that they were tracked. The black lines represent males and the grey lines represent the female. The x-axis represents the Julian day of the year

Fig. 3 Migration (**a**) duration (**b**) distance for five male and one female Asian Great Bustard (*O. t. dybowskii*) breeding in northeastern Mongolia in spring (white) and autumn (grey) between 2018 and 2020. Error bars represent 95% binomial confidence intervals

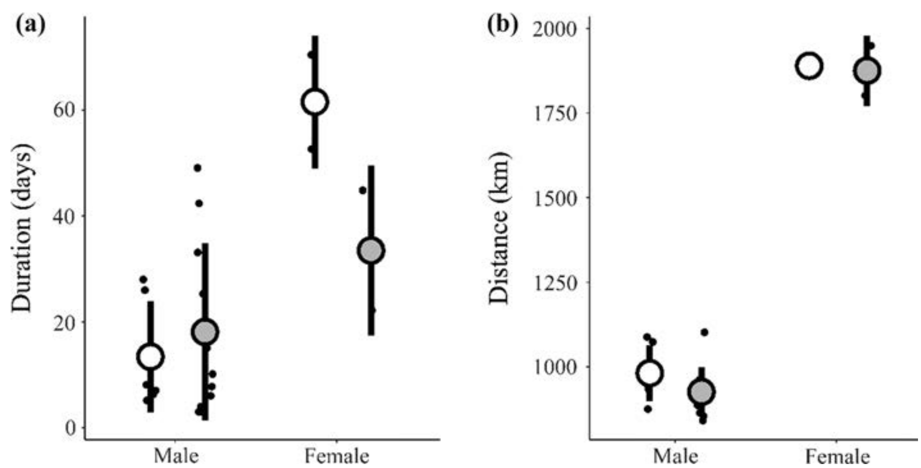
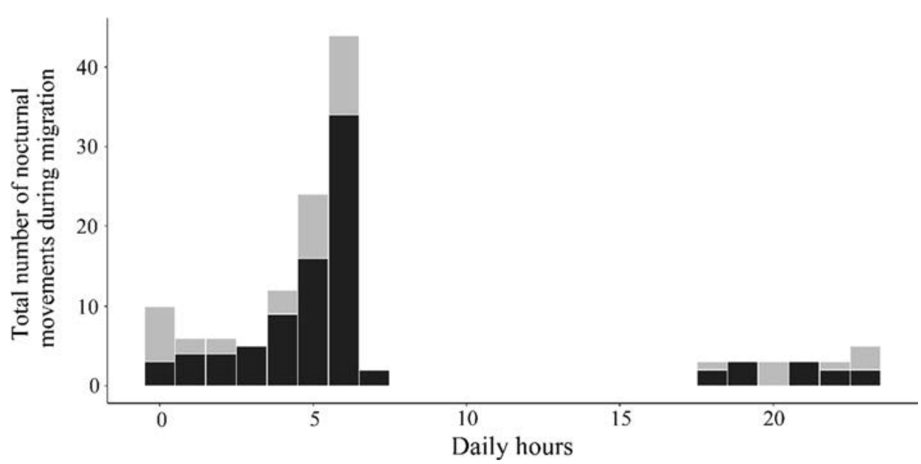


Fig. 4 Total number of nocturnal movements in every hour of five male (black) and one female (grey) Great Bustard in the eastern flyway



Movement speeds of Great Bustards in the eastern flyway

The male Great Bustards moved 121.21 ± 96.62 km/day on average during the migration season, faster than the female, which averaged 46.87 ± 23.99 km/day (Fig. 5a). The female migrated faster in the autumn than in the spring (SI, Tab. S1). The flight speed of males was close to that of the female (male: 68.19 ± 8.08 km/h; female: 63.74 ± 8.69 km/h; Fig. 5b). The travel speed of males

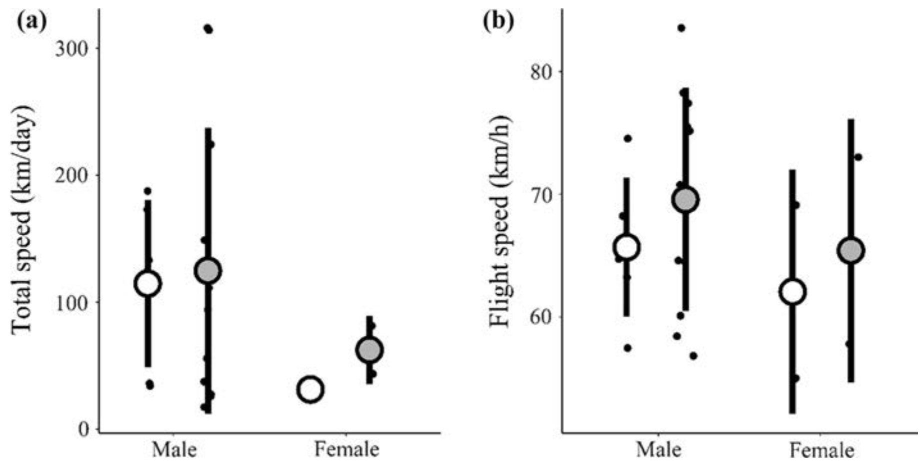


Fig. 5 Migration speed of five male and one female Asian Great Bustard (*O. t. dybowskii*) in the eastern flyway in spring (white) and autumn (grey) between 2018 and 2020, broken down by **a** total speed and **b** flight speed. Error bars represent 95% binomial confidence intervals

(186.06 ± 102.31 km/day) was slightly lower than that of the female (210.06 ± 48.25 km/day).

Stopovers

We found that the bustards tracked in this study had 39 stopovers (11 long stopovers and 28 short stopovers) in total, scattered between 40°N–50°N and 112°E–118°E (Fig. 6). Male Great Bustards stopped on average 1.53 ± 1.28 times per migration, less than the 3.50 ± 2.38 times of the female (SI Fig. S1). For each stopover site, males stayed for shorter periods than the female (male 5.84 ± 5.49 days; female 10.90 ± 12.16 days; SI Fig. S1). Males stopped 25 times in total, with 5 long stopovers in Choibalsan and Bulgan soum in Dornod province in eastern Mongolia and Inner Mongolia in China. (Fig. 6). In some cases, males stopped for less than 24 h along their whole migration route (Table 1). The lone female stopped 14 times, including 6 long stopovers in Tianjin, Hebei and Inner Mongolia in China (Fig. 6). For all individuals, only 4 long stopovers were used more than once by the three individuals in two consecutive years, respectively. The female's stop frequency was higher in autumn than in spring (SI Tab. S1). Both males and the female stopped for longer durations during the spring migration than during the autumn migration (SI Tab. S1).

Habitat fidelity and conservation gap analysis

We found that there was 66.06% average overlaps of summer ranges and a 53.28% overlap in winter ranges (Fig. 7; Table 2). In total, 22.51% (20,668/91,804) of location fixes of the study subjects occurred in protected areas (PAs), with 39.15% (19,135/48880) of breeding and post-breeding sites, 3.42% (1094/32,005) of wintering sites and 4.02% (439/10,919) of migration fixes occurring in protected areas. These PAs include eight in Mongolia and three in China. Breeding sites overlapped with Ugtam Uul Nature Reserve and Mongol Daguur Strictly PA and Landscape of Dauria (Fig. 6). For wintering, only the female bustard had fixes that were inside a PA (Huanghegudao Wetland).

Mortality

Three of six Great Bustards we tracked died (50%) during our study period. Bustard NO.1, the only female, died during the autumn migration on 27 November 2020 in Xilingol, Inner Mongolia because of a collision with an agricultural fence. Individual NO.5 died on 3 March 2019 at his wintering site because of a collision with agricultural sprinkler irrigation equipment. Bustard NO.6 died at midnight on 29 March 2020 in Xilingol due to a collision with a power line. This was the largest individual in our study (NO.6, 17.80 kg; SI, Fig. S1). And since dying, no young male has yet taken over his lek site.

Discussion

In this study, we used precise tracking data to elucidate the migration patterns of the Asian Great Bustard breeding in northeastern Mongolia and found differences between the sexes. Males started migration later but arrived earlier than the female in spring; males migrated for half as long a distance as females and spent one-third times of females in transit. Additionally, we found that the Asian Great Bustard had high site fidelity outside of migration season but that their habitats are not well protected.

Migration patterns

We found that the male Great Bustards we tracked in the eastern flyway arrived at breeding sites earlier than the single female, which may be explained by the higher intrasexual competition for mating that occurs among males.

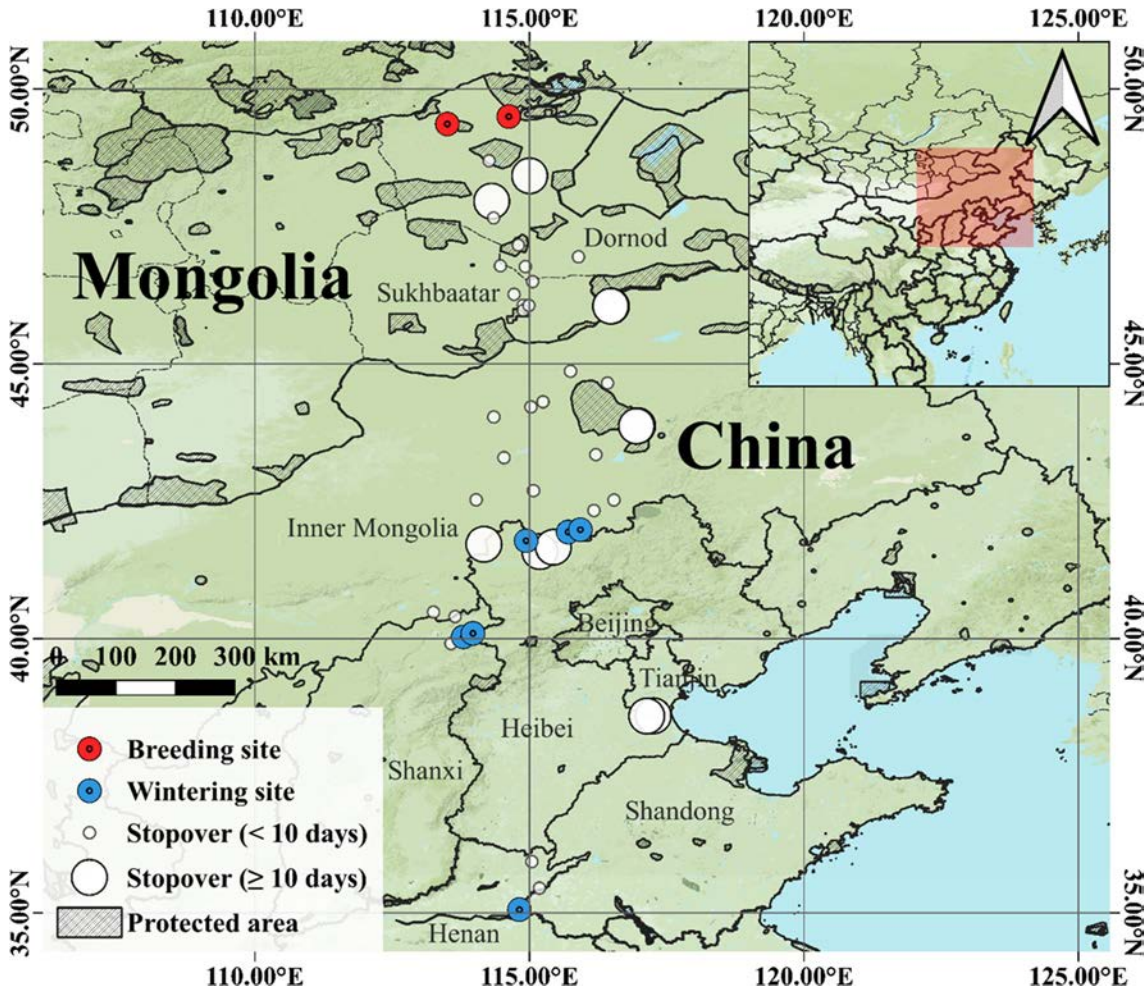


Fig. 6 Breeding, wintering, and stopover sites for six Asian Great Bustards (*O. t. dybowskii*) between 2018 and 2020

Generally in birds, males end their migration earlier than the female to acquire better breeding territories or maximize their mating opportunities (Schmaljohann et al. 2016; Briedis et al. 2019; Kissner et al. 2003; Coppack and Pulido 2009; Myers 1981; Morales et al. 2000), as also known as the arrival-time hypothesis (Myers 1981). This mechanism has been convincingly shown to be at play for the western subspecies of the Great Bustard (Morales et al. 2000; Palacín et al. 2009). We also found that these males left wintering sites later than the female. To our knowledge, this phenomenon has not been reported in other protandrous species before, because males generally initiate spring migration earlier or at the same time as females (Schmaljohann et al. 2016; Briedis et al. 2019; Kissner et al. 2003). We speculate that this phenomenon occurs because of the shorter migration distance of the males, and the long stopover time of the female during the spring migration. Considering the differences in migration distance by sex, the early departure of the female may be to compensate for the longer transit.

The Great Bustards we tracked showed sex differences in their migration distances: males migrated nearly 1000 km per route, which is about half the distance of the female. This phenomenon was similarly confirmed at the subspecies scale when combined with the data of three females from central Mongolia (Kessler et al. 2013), 1000 km (113 degrees of longitude) west of that used by the birds in our study, migrated a similar distance to our female. The wintering site of the males we tracked was 6 degrees north of the female we tracked (Fig. 1), with the males wintering farther north. Males wintered closer to their breeding sites, which contributed to bustard's ability to return to the breeding site in a shorter amount of time, no doubt helping them cope with the intrasexual competition (Coppack and Pulido 2009). Besides, high sexual size dimorphism influences their tolerance to environmental conditions, such as cold weather. Ketterson (1976) found that larger birds can remain in harsher environments closer to the breeding grounds, whereas smaller individuals are constrained by winter chills and need to migrate farther. In our study, male *O. t. dybowskii*

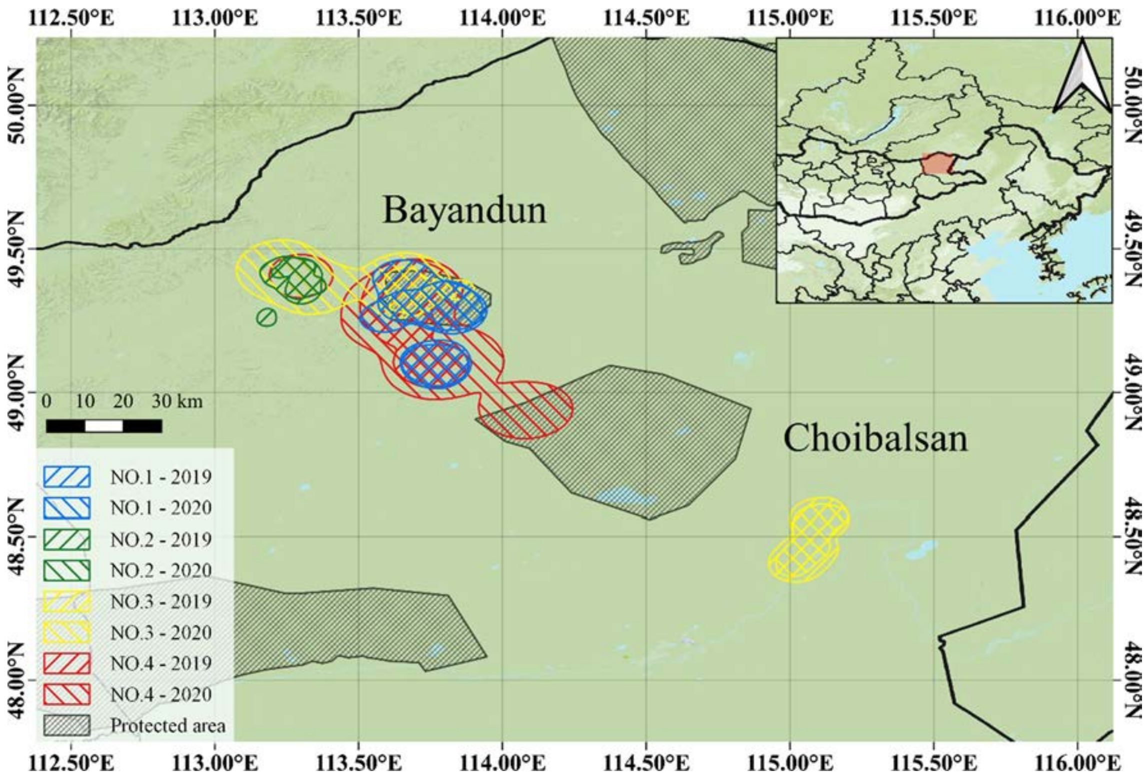


Fig. 7 A map showing the overlaps of breeding and post-breeding sites of four individuals (3 males and 1 female) in the summers of 2019 and 2020, in Dornod province, Mongolia

Table 2 Areas of 95% KDE home range (km^2) of *O. t. dybowskii* and overlaps in two consecutive years (proportion)

ID	Sex	2019 summer	2020 summer	Overlaps	2018 winter	2019 winter	Overlaps
NO. 1	Female	816.48	645.53	0.774	1261.21	177.38	0.214
NO. 2	Male	237.33	138.65	0.705	14.90	19.42	0.699
NO. 3	Male	649.47	1377.80	0.520	96.08	26.50	0.486
NO. 4	Male	841.79	2110.22	0.643	19.36	27.05	0.692

weighed 12.24 ± 3.14 kg on average, which is approximately 2.9 times that of the female (Table 1), and overwinter north than the female. We extracted average monthly temperatures at wintering sites of both sexes from October to April in 2018–2020 (National Earth System Science Data Center, National Science & Technology Infrastructure of China, http://www.geodata.cn). We found that the average monthly temperature of male wintering sites was about 10 ℃ lower than that of the female (SI, Tab. S3), which was consistent with this hypothesis.

Further, males may winter in Mongolia for some years, depending on weather conditions and snow cover. For example, Mongolian researchers observed four overwintering male Great Bustards near croplands in northern central Mongolia, on 15 January 2005 (Batsaikhan, N. personal communication) and 17 Great Bustards in western Mongolia, on 31 January 2004 (Batdemberel, D. personal communication). Natsagdorj (2001) also notes Great Bustards as being present in Mongolia in winter. These observations likely underscore the physiological limitations of body size and the reason for the different migration distances of the two sexes.

The migration distance of the Great Bustard also varies between subspecies. We found the migration distance of males we monitored was over 10 times longer than males in Spain (Palacín et al. 2009). The male and female Great Bustards in this study moved up to 540 km and 594 km in one day, respectively, which was longer than the maximum distance per day reported for the western subspecies recorded in Russia (maximum 325 km per day) (Watzke 2007). Kessler et al. (2013) considered that migratory distances increase longitudinally from west to east across the range of this species because of the harsh environmental conditions in Asia. Our results were in line with this hypothesis.

In addition, we found females spent more days in spring than autumn during migration, which may be caused by the long stopover duration in spring (Kessler et al. 2013). Temperature and wind support mainly trigger the migration movement of the Great Bustard (Kessler 2015; Streich et al. 2005). In northern China and Mongolia, weather condition remains harsh and unstable in March. Thus, females may wait at stopovers until the environmental conditions become more comfortable (Kessler 2015). Further, female Great Bustards incubate eggs and raise chicks singly in summer (Kessler 2015), so a long stopover duration provided enough time for energy replenishment for egg production in the breeding season (Tourenq et al. 2004).

We also found Great Bustards exhibited occasional night movement during migration. Long-distance nocturnal migrations may explain why male great bustards we tracked can complete long-distance migrations in a very short period of time. The Great Bustard usually roosts when darkness falls, but occasionally conducts nocturnal activity in spring or winter (Morales and Martín 2002). However, few studies described the nocturnal migratory behaviours of great bustards to our knowledge (Raab et al. 2014). Diurnal species have flexibility in circadian timing strategies during migration (Newton 2008) when they are crossing inhospitable terrain or with comfortable atmospheric conditions (Martin 1990). Besides, feeding is the most time-consuming activity for great bustards (Martínez 2000). Thus, another possibility for nocturnal migration is that migratory flights at night do not interfere with foraging during the days (Lank 1989; Fusani and Gwinner 2005).

Habitat fidelity and distribution

We found that all four individuals tagged in northeastern Mongolia for which we have more than one year of tracking data showed strong site fidelity (over 50%) during both wintering and breeding seasons. Understandably, both females and males gathered in the breeding season, given the breeding displays and mating behaviour of the species. Males first aggregate, showing ground-displaying behaviour in a high visibility area to attract females (Alonso et al. 2012), and then form dispersed leks (Morales and Martín 2002). This high lek site fidelity was also found in the western subspecies (Alonso et al. 2000).

Our tracking data revealed that Asian Great Bustards using the eastern flyway have three different wintering sites including Xinxiang, Henan, Xilingol, Inner Mongolia and a previously unknown wintering site in Datong, Shanxi; two breeding sites in Bayandun and Dashbalbar in Dornod province; and one newly found post-breeding site in Choibalsan Soum in Dornod Province (Figs. 1 and 6). The stopover sites during migration for each individual were random and scattered, similar to what has been observed for the population in central Mongolia (Kessler 2015). New migration stopover sites were found in Choibalsan and Bulgan Soums in Dornod Province in Eastern Mongolia, and Tianjin, Zhangjiakou, Hebei and Xilingol, in Inner Mongolia in China. Given that these newly discovered sites were determined from tracking just six individuals, we strongly suspect that Asian Great Bustards may utilize a greater number of sites across their annual range than previously understood.

Conservation recommendations

Our results have revealed that only one breeding and one wintering site used by our tracked Asian Great Bustards are inside a protected area and that there is generally a low overlap between their home ranges and PAs, with large numbers of stopover habitats occurring far outside existing nature reserves (SI Fig. S1). During winter and migration season, Great Bustards spend less than 5% of their overall time in the protected areas, indicating the protection of the Great Bustard's habitat is inadequate. In addition, it may be difficult for this species to adapt to a changing environment given its high site fidelity. We recommend establishing more protected areas at wintering sites. The local government should increase residents' awareness and co-manage with them to protect this valuable species, especially at stopovers. Additionally, more research is urgently required to assess habitat quality for Great Bustards and develop efficient plans to provide suitable habitat for the species.

Great Bustards are threatened by predators and sensitive to human disturbance (Morales and Martín 2002), suffering rapid population reductions across most of their range owing to hunting, powerline collisions, and degradation and fragmentation of their habitat (IUCN 2017). The deaths we observed demonstrate the high mortality risk faced by this species: In two years, half of the Great Bustards we tracked died in their wintering sites or during migration, which was the same as the Great Bustard tracked in central Mongolia (Kessler 2015). The Great Bustard is thought to be a "poor" flier and has experienced record numbers of powerline collision casualties in recent years (Janss 2000). Powerline marking is an effective way to reduce the collision mortality of most birds. However, it showed little or no benefit for bustards (Shaw et al. 2021; Alonso et al. 1994; Marques et al. 2020). Thus, we suggested rerouting or undergrounding powerlines in areas where Great Bustards are densely distributed to eliminate collisions, especially on the migratory pathways and overwintering sites. International cooperation is also needed to protect this endangered species effectively.

Limitations

Some constraints exist for our study. First, we tracked six adult bustards with one female, which may limit our analysis. However, we found similar trends in migration distance after adding migratory data of three females from Kessler et al. (2013). Second, environmental factors (Alonso et al. 2009a) or refuelling patterns (Dierschke et al. 2004) may also affect animals' migration rhythm. We cannot exclude the effect of the above factors on sex differences in these subspecies. Besides, the Great Bustard is distributed widely in Mongolia, and the migration routes vary among populations. However, we only tracked one of those populations. Thus, future studies will need to be conducted in more areas to completely reveal the migration patterns of Great Bustards and provide a more generalizable insight for comprehensive conservation.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10336-022-02030-y.

Acknowledgements We thank Yun yan, Xilin Gol League Forest Public Security for helping us with fieldwork and Professor Xinhai Li for guidance in the statistical calculation. We thank the long-term support of the National Forestry and Grassland Administration. We thank Dr. Tim Treuer at Princeton University for his assistance with the English language and grammatical editing. Special thanks to our hardworking driver Bundaa and local herder family Khurelee in the Ugtam area.

Author contributions YG conceived the project idea and contributed substantial materials, resources, and funding. GP, AG, BE, OT, DK, ZW and YG carried out fieldwork. YW and CM analysed and visualized the data. YW drafted the manuscript with the support of GP, CM and YG. All authors read and approved the final manuscript.

Funding This work was supported by the National Natural Science Foundation of China (No. 31770573).

Data availability The datasets generated during and/or analysed during the current study are not publicly available for protecting the vulnerable eastern subspecies of Great Bustard, but are stored at Movebank (www.movebank.org) in the study "Great Bustard (*Otis tarda dybowskii*) in Northeast Asia" (Movebank Study ID: 2225327907) and can be made available by the author upon reasonable request.

Code availability The analyses generated during the current study are available on reasonable request.

Declarations

Conflict of interest The authors declare that they have no competing interests.

Ethical approval The study was performed under the licences of the Ministry of Nature, Environment and Tourism of Mongolia (Ethics approval number: 10).

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