The importance of the Qinghai-Tibet Plateau for Bar-headed Geese *Anser indicus*: results from GPS/GSM telemetry

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Abstract

The Bar-headed Goose *Anser indicus* is confined to central Asia, where it is currently increasing in abundance. Historically, the species has been divided into seven flyway units, of which the Eastern Flyway comprises 70% of the total world population. We used data from GPS-GSM transmitters deployed on Eastern Flyway Bar-headed Geese to differentiate between sub-populations exhibiting contrasting migration strategies and to assess the importance of the Qinghai-Tibet Plateau (QTP) for these sub-populations. Tracking results identified three distinctive sub-populations with differing migration patterns within the flyway. These were: 1) the Qinghai Lake–Shigatse Prefecture sub-population, short-distance migrants; 2) the Mongolia–Shigatse Prefecture sub-population, middle-distance migrants; and 3) the Mongolia–India/Bangladesh sub-population, long-distance migrants. Individuals in the short-distance sub-population remained in the QTP throughout the entire annual cycle. The middle-distance sub-population also exploited the QTP but returned north to Mongolia to breed. Geese from the long-distance sub-population departed their Mongolian breeding grounds early and spent > 80% of the total migration duration within the QTP, despite this area constituting less than half the total migration distance during both autumn and spring migration. These results show that birds from all three sub-populations have a particular affinity for the QTP, confirming the importance of this area to all sub-populations of Eastern Flyway Bar-headed Geese. Migration among birds from the long-distance sub-population was significantly faster in spring than in autumn, the result of using fewer stopover sites and a shorter total stopover duration. We recommend more telemetry studies to confirm these patterns and support improved protection of site networks. Further ground surveys of Bar-head Goose numbers are also required to identify threats to staging and wintering areas used by the different sub-populations of Bar-headed Geese in Eastern Flyway, with a view to securing key sites for the future.

Key words: *Anser indicus*, Bar-headed Goose, migration distance, migration duration, step length.

Defining discrete flyway populations of migratory bird species is important for understanding their underlying population structure, which is vital for their effective conservation management (Moritz 1994). Geese of the same species show relatively high levels of site loyalty, especially to natal areas (Greenwood & Harvey 1982; Rohwer & Anderson 1988; Anderson *et al.* 1992). As a result, conspecifics which use different regions in the course of their annual cycle may show differences in timing of migration, stopover duration and body store accumulation for investment in migration and breeding, which ultimately restrict gene flow between birds from different regions (*e.g.* Li *et al.* 2020a). Reduced levels of connectivity between individuals of the same species may ultimately lead to sub-speciation and speciation in natural populations (*e.g.* the contrasting levels of morphological differentiation in the circumpolar Greater White-fronted Geese *Anser albifrons*; Ely *et al.* 2005) and so can have evolutionary implications (Rockwell & Barrowclough 1987). From a conservation standpoint, we need to take into account such distinctions between sub-populations when considering factors such as hunting regulation, protected area designation and management that differentially affect different elements of a species, which behave differently and which may be separated at different stages of the annual cycle (*e.g.* Szczys *et al.* 2017). This is important, because we need to recognise the different environmental factors affecting demographic processes in the separate flyway units on developing conservation interventions, as for example in the four different management units recognised for the Taiga Bean Geese *Anser fabalis* in Europe (Johnson *et al.* 2017). Where species begin to develop differential migration strategies between allopatric breeding and/or wintering areas, sub-populations may increasingly show differences in their timing and duration of migration episodes, as well as the periods of fattening that are associated with migration and breeding, and where the birds chose these critical phases to take place (*e.g.* Li *et al.* 2020a). As a result, ultimately the timing and speed of migration in separate segments of what was formally one species population may come to differ to meet the specific seasonal demands of birds that travel between different breeding and wintering areas (*e.g.* Li *et al.* 2020a). Furthermore, differential migration patterns and exploitation of geographically discrete environments could potentially have fitness consequences, by contributing to differences in survival rates and reproductive success, ultimately affecting trends in population sizes (as, for example, between Bewick's Swans from the Northwest European and East Asian populations; Cong *et al.* 2011). Despite this, our knowledge and understanding of the differences in migration patterns between different sub-populations of the same species in some cases remain rudimentary.

The Bar-headed Goose *Anser indicus* is recognised as being markedly different to other goose species in Asia, particularly because of its physiological adaptations for flying at altitudes of over 6,000 m, where oxygen pressure is very low (Hawkes *et al.* 2011, 2013, 2017; Bishop *et al.* 2015). As illustrated by many previous telemetry studies (Prosser *et al.* 2009; Bourouiba *et al.* 2010; Hao *et al.* 2010; Köppen *et al.* 2010; Guo-Gang *et al.* 2011; Prosser *et al.* 2011; Newman *et al.* 2012), the Bar-headed Goose appears to have seven major migration flyway units (Fox & Leafloor 2018). Of these, geese from the Eastern Tibetan Migration Flyway (hereafter "Eastern Flyway") breed in western Mongolia, the southeast Xinjiang Uygur Autonomous Region and the Qinghai-Tibet Plateau (hereafter QTP), China (Zhang *et al.* 2020). More than 70% of the world population winters in this flyway, distributing throughout the southern part of the QTP, continuing south to winter in Nepal, India and eastwards to the Yunnan-Guizhou Plateau (Bishop *et al.* 1997; Javed *et al.* 2000; Takekawa *et al.* 2009; Yang & Zhang 2014; Liu *et al.* 2017). In the Western Tibetan Migration Flyway (hereafter "Western Flyway"), the geese breed in southeast Kyrgyzstan, Kazakhstan and the northwest Xinjiang Uygur Autonomous Region in China, and winter in Pakistan and the western Indian subcontinent (Köppen *et al.* 2010; Takekawa *et al.* 2017).

The global population of Bar-headed Geese was estimated from wintering ground counts to be 50,000–65,000 individuals in 2010 (Van der Ven *et al.* 2010), but larger numbers have recently been found apparently short-stopping along the Yarlung Zangbo River in the Eastern Flyway, suggesting that the true total is *c.* 97,000–118,000 birds (Liu *et al.* 2017). It is unclear whether this represents a genuine increase in the population size or the result of shifts in distribution that facilitates easier counting.

In the Western Flyway, Bar-headed Geese from Kyrghyzstan were tracked in 1998 to wintering grounds in Pakistan, India and Uzbekistan, using southern Tajikistan and the western QTP as stopover areas, with results indicating that this sub-population adopts a time-minimisation strategy in spring and an energy-minimisation strategy in autumn (Köppen *et al.* 2010). However, although the Eastern Flyway supports greater numbers of Bar-headed Geese, previous studies in this flyway have not explored how different elements of the Bar-headed Goose sub-populations migrate in relation to their departure dates, speed of migration along their respective corridors, and the relative importance of stopover staging areas on the migration routes. For example, telemetry-tracking by Takekawa *et al.* (2009) demonstrated that Bar-headed Geese undertook a leap-frog migration from Mongolian breeding grounds to wintering sites in Northern India, while those geese breeding at Qinghai Lake further south in China wintered in the southern part of the QTP, but staging frequency and locations were not described in detail. Some migration parameters (including depart date, arrival date, migration duration, number of stopover sites and step length) of tagged Bar-headed Geese breeding in Qinghai Lake and wintering in the southern part of the QTP during 2007–2009 were reported by Prosser *et al.* (2011). Given the patchy and highly dispersed nature of the species, however, as well as recent shifts in its wintering provenance, there is a need to clarify the sub-population structure of this iconic but poorly understood species. Bar-headed Geese breeding together in Mongolia are known to undertake migrations of differing duration to winter in different areas, so we were especially keen to contrast departure dates and speed of migration between individuals flying different migration distances, including those birds which are known to move only within the QTP. In this study, we therefore used telemetry to compare the migration schedules of long, middle and short-distance migration patterns amongst the Eastern Flyway population of Bar-headed Geese that migrates between different areas from Mongolia, through central China, to the QTP and the Indian sub-continent.

Methods

Satellite tracking data

Backpack GPS–GSM transmitters were fitted to 27 Bar-headed Geese rounded up and captured in western Mongolia, at Terkhiin Tsagaan Lake (48.15°N, 99.59°E) and at Bayan Lake (49.94°N, 93.90°E) during the flightless moult period in 2018 (see Table 1 for full details). Heavier devices were deployed on neck collars to three geese rescued by the Qinghai Lake National Nature Reserve Rescue Centre, China (37.07°N, 99.82°E) in 2016 (Zhang *et al.* 2020). Deployment of different devices, with different attachment methods and frequency of positions, to wild and rehabilitated geese in different seasons adds a layer of difficulty in making direct comparisons between these two samples. However, given the highly restricted numbers of tracked Bar-headed Geese in the region, we consider it necessary to present all derived data to support our improved understanding of the species. Furthermore, although we cannot eliminate the possibility that the fitted devices affected the behaviour and ecology of these individuals, the loggers constituted < 3% of an individual's total body mass, so were below the weight at which devices are considered more likely to have an adverse effect on the birds (Millspaugh & Marzluff 2001; Lameris & Kleyheeg 2017; Bodey *et al.* 2018). Devices attached in 2018 and 2016 were set to record the GPS locations with time and date stamp at 10 min and 2 h intervals throughout the research project, respectively.

Defining and analysing migration parameters

We defined autumn migration as starting from the first position after tagged individuals departed from the summering grounds and terminating with the first position of a series of positions received from the wintering grounds. Likewise, spring migration was defined on similar criteria for the return to the breeding areas.

We applied the methods of Wang *et al.* (2018) to segment movement tracks, identifying flight legs between successive stopover sites, which were defined as locations where a bird did not move > 30 km over a 48 h period (Kölzsch *et al.* 2016). For migration parameters, we applied the definitions of Deng *et al.* (2019) and Li *et al.* (2020b). We defined departure date as the date of the first position when a bird left summering/wintering sites, and arrival date as the date when a bird was determined to have arrived at wintering/summering sites after a period of flight. Migration duration was defined as the total duration of spring and autumn migrations, including the periods spent at stopover sites. We defined migration distance as the cumulative travel distance between all adjacent GPS locations, which were identified as "non-stopover" status during migration. Migration speed was calculated as migration distance divided by migration duration. The number of stopover sites throughout each migration episode was calculated using the criteria above to define how many times Bar-headed Geese used separate stopover sites. Stopover duration was defined as the sum of all days spent at all stopover sites during each migration season. Thus, the actual number of travelling days (travel duration) was calculated by subtracting total stopover duration from total migration duration and the daily travel speed was calculated by dividing cumulative migration distance by travel duration. We calculated step length as the migration distance divided by the number of flight legs (similar definition with the number of stopover sites) during each migration season, and the straightness index as the path tortuosity of the movement between summering and wintering areas relative to the shortest path in both directions (Benhamou 2004).

Parameters analysis

Initial inspection of the data showed three distinctive migration strategies among our tagged birds, which we here assign to "sub-populations", because of their distinguishing spatial and temporal patterns. The telemetry immediately showed that individual Bar-headed Geese exhibited different summering/staging/wintering area connectivity, which we classified according to the following categories: 1) the Qinghai Lake (Qinghai Province, China)–Shigatse Prefecture (Tibet Autonomous Region, China) sub-population, short-distance migrants (hereafter TtoT); 2) the Mongolia–Shigatse Prefecture sub-population, middle-distance migrants (MtoT); and 3) the Mongolia–India/ Bangladesh sub-population, long-distance migrants (MtoA) (see Fig. 1). We quantified the migration parameters within QTP,

Table 1. Summary table of Bar-headed Geese fitted with solar–powered GPS/GSM telemetry devices, which provided data used in the current analysis.

Bird ID	Autumn migration	Spring migration	Sex	Age	Body mass (g)	Capture site	Capture month and year	Device manfacturer	Device type	Device mass (g)	Device mass/ body mass
Completed autumn migration											
QHL_2	***	*	?	?	?	Qinghai Lake, China	Jun. 2016	HGMT	Neck collar	40.0	–
QHL_3	***	*	?	?	?	Qinghai Lake, China	Jun. 2016	HGMT	Neck collar	40.0	–
MON_1[a]	***	*	?	A	2,070	Bayan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.3%
MON_4[a]	***	**	M	A	2,510	Bayan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.1%
MON_5	***	*	M	A	2,950	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	0.9%
MON_7	***	***	M	A	2,700	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.0%
MON_8	***	***	M	A	2,350	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.2%
MON_12	***	**	M	A	2,360	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.2%
MON_14	***	***	F	A	2,200	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.3%
MON_16	***	**	F	A	2,380	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.2%
MON_18	***	*	M	A	2,720	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.0%
MON_20	***	***	M	A	2,500	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.1%
MON_22	***	**	F	A	2,520	Bayan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.1%
MON_23	***	*	M	A	2,500	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.1%
MON_25	***	*	F	A	2,480	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.1%

Bird ID	Autumn migration	Spring migration	Sex	Age	Body mass (g)	Capture site	Capture month and year	Device manfacturer	Device type	Device mass (g)	Device mass/ body mass
Incomplete autumn migration											
MON_3	**	*	F	A	2,000	Bayan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.4%
MON_9	**	*	F	A	2,305	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.2%
MON_10	**	*	F	A	2,540	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.1%
MON_11	**	*	F	A	2,080	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.3%
MON_19	**	*	F	A	2,320	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.2%
MON_24	**	*	?	A	1,960	Bayan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.4%
MON_27	**	*	M	A	2,580	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.1%
Without migration data											
QHL_1	*	*	?	?	?	Qinghai Lake, China	Jun. 2016	HGMT	Neck collar	40.0	–
MON_6	*	*	M	A	2,780	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.0%
MON_13	*	*	M	A	2,420	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.1%
MON_15	*	*	M	A	2,250	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.2%
MON_17	*	*	F	A	2,020	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.4%
MON_21	*	*	?	A	2,470	Bayan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.1%
MON_26	*	*	?	A	2,410	Terkhiin Tsagaan Lake, Mongolia	Jul. 2018	Ornitela	Backpack	27.5	1.1%

For three geese captured in Qinghai Lake 2016, age, sex and body mass on capture are unknown. All 27 geese captured in Mongolia 2018 are adult, including 13 male, 10 female and 4 unknown sex. Mass of the backpack-mounted logger includes 2.5 gm of Teflon ribbon. *** = full migration data, ** = data lost during migration, * = without migration data. [a] = birds which migrated together.

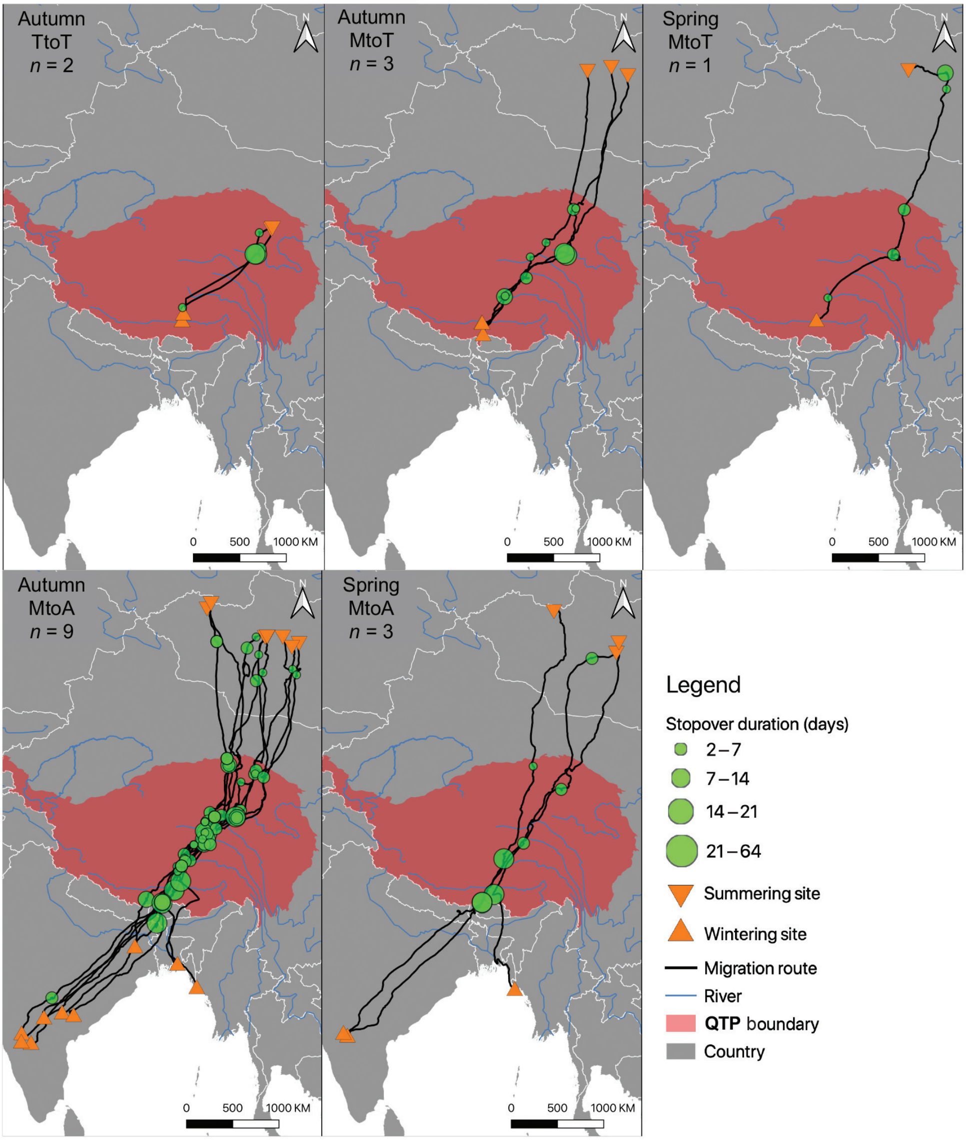

Figure 1. Autumn and spring individual migration routes (black lines) and stopover sites (green circles) of Bar-headed Geese derived from GPS/GSM telemetry devices deployed on birds tracked in autumn 2016, autumn 2018 and spring 2019. The area shaded red shows the Qinghai–Tibet Plateau. TtoT = Qinghai Lake–Shigatse Prefecture routes; MtoT = Mongolia–Shigatse Prefecture routes; MtoA = Mongolia–India/Bangladesh routes. Sample sizes (*n*) are the number of individuals tracked over a full migration. Figure is reproduced from Zhang *et al.* (2020).

starting when geese arrived at the QTP or departed breeding/wintering grounds and ending when geese departed the QTP or arrived at the wintering grounds, to compare with the same parameters gathered from birds undertaking the full migration routes. We assessed seasonal differences for the nine migration parameters (migration duration, migration distance, migration speed, number of stopover sites, stopover duration, travel duration, daily travel speed, step length, straightness index). Because of the limited sample size, we were able to make these comparisons between spring and autumn migration parameters only for the MtoA sub-population. To avoid pseudo-replication, we selected only one bird from two individuals in the MtoA sub-population that accompanied each other on migration (indicated with ^{a} in Table 1). For parameters with small sample sizes, we tested for differences between measures by applying Mann-Whitney U test; otherwise we applied ANOVA (after applying Bartlett tests to test for equal variances and multiple range tests) in cases where sample sizes were adequate and data normally distributed. All statistical analyses were conducted in R 3.6.0 (R Core Team 2019).

Results

In total, data were obtained from individuals that completed 14 autumn migrations and four spring migrations. Two birds from Bayan Lake, Mongolia migrated together and so are treated as one individual. In the following results we present the number of birds (*n*) for each autumn and spring migration from which we had a full set of tracking data to contribute to each of the analyses. All the routes followed by the tracked birds are shown in Fig. 1.

Geese from all sub-populations spent a major proportion of their migration period at the QTP, irrespective of the total migration distances undertaken (see Table 2). For instance, during autumn, 84%–100% of the migration time for each of the three populations was spent at the QTP. Geese from the Mongolia–India/Bangladesh (MtoA) sub-population took on average of 85.7 days (s.d. ± 19.5 days, *n* = 9 individuals) to complete their 4,667.9 km (± 658.0) migration, of which 72.3 ± 17.3 days (84% of the total migration duration, and 88% of their stopover duration) were spent at the QTP, which in contrast accounted for 2,148.6 ± 313.9 km (46%) of the total migration distance. The proportion of the total migration duration that the MtoA geese spent at the QTP therefore was longer than the proportion of the distance involved. Although geese from the Mongolia–Shigatse Prefecture, China sub-population (MtoT, *n* = 3) had a shorter migration route of 2,893.3 ± 84.5 km to their ultimate wintering areas at the QTP (of which 1,835.7 ± 65.7 km, 63%, were at the QTP), they also spent all of their stopover time and almost all of migration duration at the QTP (44.9 ± 5.5 days out of 45.9 ± 6.7, 98%). The proportion of time at the QTP therefore was again markedly longer than the proportion of the distance travelled to their ultimate wintering areas on the southern fringe of the Himalayas. Geese from the TtoT sub-population (*n* = 2), which bred on Qinghai Lake and wintered in the southern fringe of the Himalayas, spent all of their annual cycle life within the QTP.

Table 2. Summary parameters comparing data over entire migration episodes with those from within the QTP for Bar-headed Geese tracked in autumn 2016, autumn 2018 and spring 2019, reported by season and migration route (*n* = no. of geese tracked). TtoT = birds from the Qinghai Lake–Shigatse Prefecture sub-population, MtoT = the Mongolia–Shigatse Prefecture sub-population and MtoA = the Mongolia–India/Bangladesh sub-population, as described in the text. Both TtoT transmitters failed before spring migration; hence the absence of data. QTP = Qinghai-Tibet Plateau.

Season	**Route (*n*)**	**Data description**	**Depart (summer)**	**Arrive (QTP)**	**Depart (QTP)**	**Arrive (winter)**	**Migration duration (days)**	**Migration distance (km)**	**No. stopovers**	**Stopover duration (days)**	**Travel duration (days)**	**Step length (km)**
Autumn	MtoA ($n = 9$)	Entire migration	1 Sept.			25 Nov.	85.7	4,667.9	6.4	76.9	8.8	642.9
		Within QTP only		8 Sept.	19 Nov.		72.3	2,148.6	5.3	67.3	5.0	356.0
		% in QTP					84%	46%	83%	88%	57%	55%
	MtoT ($n = 3$)	Entire migration	13 Sept.			29 Oct.	45.9	2,893.3	3	41.4	4.4	883.8
		Within QTP only		14 Sept.	29 Oct.		44.9	1,835.7	3	41.4	3.5	553.4
		% in QTP					98%	63%	100%	100%	78%	63%
	TtoT ($n = 2$)	Within QTP only	26 Aug.			12 Nov.	78.0	1325.1	2.5	70.7	7.3	387.9
		% in QTP					100%	100%	100%	100%	100%	100%
Season	**Route (*n*)**	**Data description**	**Depart (winter)**	**Arrive (QTP)**	**Depart (QTP)**	**Arrive (summer)**	**Migration duration (days)**	**Migration distance (km)**	**No. stopovers**	**Stopover duration (days)**	**Travel duration (days)**	**Step length (km)**
Spring	MtoA ($n = 3$)	Entire migration	9 Mar.			30 Apr.	51.3	4,685.2	2.7	44.8	6.4	1,314.2
		Within QTP only		12 Mar.	25 Apr.		44.3	1,804.7	2.3	41.2	3.2	555.7
		% in QTP					86%	39%	88%	92%	49%	42%
	MtoT ($n = 1$)	Entire migration	4 Apr.			6 Jun.	62.2	3,197.5	5.0	55.7	6.5	532.9
		Within QTP only		4 Apr.	8 May		33.1	1,768.5	3.0	29.6	3.5	442.1
		% in QTP					53%	55%	60%	53%	54%	83%

These had the shortest migration route (1,325.1 ± 48.5 km) and took 78 days (± 1.6) to complete their autumn migration. Only geese from the MtoA sub-population (*n* = 3) were tracked on spring migration, but these spent 86% of the migration duration (44.3 ± 7.1 days in a total of 51.3 ± 9.2 days) to cover the 39% of the migration distance (1,804.7 ± 175.8 km of 4,685.2 ± 724.9 km) within the QTP. Sample sizes are small but the results indicate that, as in autumn, the geese spent markedly more time at the QTP during spring migration in relation to the distances involved.

Departure dates of MtoA geese leaving their breeding grounds in west Mongolia (1 September ± 11 days) did not differ from those of MtoT geese (13 September ± 6 days, Mann-Whitney U test: W = 4, P = 0.10, n.s.). Although the average migration distance completed by MtoA geese was 1.6 times that of MtoT geese, their migration speed and daily travel speed did not differ (W = 10, P = 0.60, n.s.). The migration speed and daily travel speed of MtoA geese were 57.1 ± 14.7 km/day and 550.5 ± 120.9 km/day, respectively, compared to MtoT geese (64.0 ± 9.8 km/day and 662.1 ± 97.0 km/day). By comparison, the migration speed (17.0 ± 1.0 km/day) and daily travel speed (198.8 ± 77.9 km/day) of TtoT geese were between a third and a quarter of those of the MtoA and MtoT geese (see Fig. 2 and Table 2). Although the autumn migration distance of MtoA geese was 3.5 times longer than that of the TtoT geese, their migration duration differed significantly (Mann-Whitney U test: W = 18, $P < 0.05$), due to the similar stopover duration, which was the main determinant of migration duration. MtoA geese spent 76.9 days on staging (88% within QTP) at 6.4 stopover sites, which did not differ significantly from the 70.7 days recorded for the TtoT geese (100% within QTP; adj. P = 0.83, n.s.) at 2.5 stopover sites, but was significantly longer than the 41.4 days of the MtoT geese (100%; adj. P = 0.01; ANOVA: $F_{2,\,11} = 6.27$, $P < 0.05$) at 3.0 stopover sites. Travel duration is another component of the overall migration duration, albeit a relatively small one in comparison with time spent staging at stopover sites. MtoA geese spent 8.8 days in travel duration (57%), which did not differ from the 7.3 days recorded for the TtoT geese (100%; adj. P = 0.6, n.s.), but was significantly longer than the 4.4 days of the MtoT geese (78%; adj. P = 0.02; ANOVA: $F_{2,\,11} = 5.15$, $P < 0.05$; see Table 2).

On comparing autumn and spring migration parameters of MtoA geese, we found that the Bar-headed Geese migrated less rapidly in autumn than in spring. Autumn migration duration, the number of stopover sites, mean stopover duration and travel duration were all significantly greater than the same parameters in spring ($P < 0.05$), while migration speed and step length during autumn migration was significantly shorter than in spring (Mann-Whitney U test: W = 25 and 27, respectively, $P < 0.05$; see Table 3 and Fig. 2). The migration distance, daily travel speed and the straightness index did not differ significantly between autumn and spring migrations (Table 3). In general, for the similar migration distance, the migration duration of Bar-headed Geese was less in spring than autumn, the result of fewer stopover sites, shorter stopover and travel

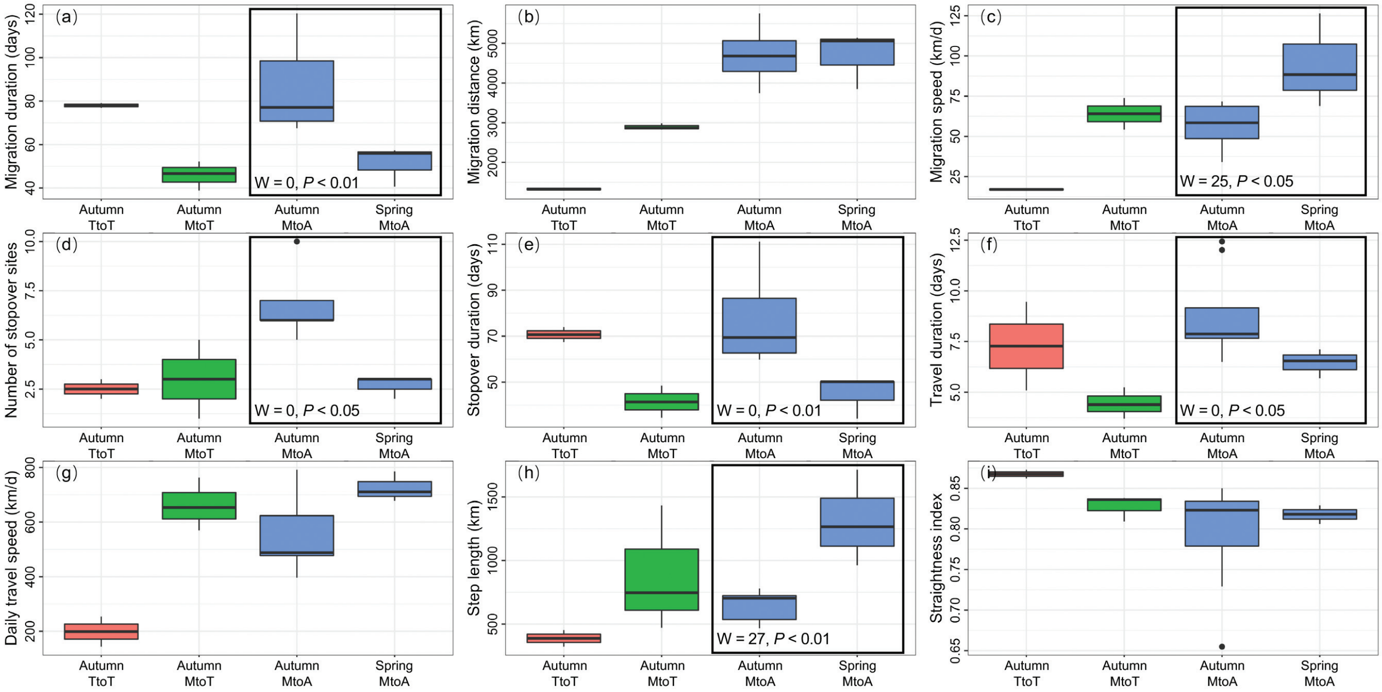

Figure 2. Box plot summaries of migration parameters for tagged TtoT (Qinghai Lake–Shigatse Prefecture), MtoT (Mongolia–Shigatse Prefecture) and MtoA (Mongolia–India/Bangladesh) Bar-headed Geese: (a) migration duration; (b) migration distance; (c) migration speed; (d) number of stopover sites; (e) stopover duration; (f) travel duration; (g) daily travel speed; (h) step length; (i) straightness index of the migration path. TtoT geese are represented in red, MtoT geese in green, and MtoA geese in blue. Full migration parameters for individual birds are reported in Table S1 and results of statistical tests in Table 3.

Table 3. Mean values (± s.d.) and Mann-Whitney U tests comparing the migration parameters of tagged MtoA Bar-headed Geese recorded during autumn 2018 and spring 2019. Bold font indicates a significant difference in migration parameter between autumn and spring. Full migration parameters for individual birds are reported in Supporting Materials Table S1. Each migration parameter is defined in the *Methods* section.

Parameters	**Mean values (mean ± s.d.)**		**Mann-Whitney U test**	
	Autumn	**Spring**	**W**	***P* value**
Departure date	Sept 1 ± 11 days	Mar 9 ± 6 days	–	–
Arrive date	Nov 25 ± 17 days	Apr 30 ± 12 days	–	–
Migration duration (days)	**85.7 ± 19.5**	**51.3 ± 9.2**	**0**	**< 0.01**
Migration distance (km)	4,667.9 ± 658.0	4,685.2 ± 724.9	15	0.864
Migration speed (km/d)	**57.1 ± 14.7**	**94.6 ± 29.3**	**25**	**< 0.05**
Number of stopover sites	**6 ± 2**	**3 ± 1**	**0**	**< 0.05**
Stopover duration (days)	**76.9 ± 18.8**	**44.8 ± 9.3**	**0**	**< 0.01**
Travel duration (days)	**8.8 ± 2.1**	**6.4 ± 0.7**	**0**	**< 0.05**
Daily travel speed (km/d)	550.5 ± 120.9	724.7 ± 55.4	24	0.064
Step length (km)	**642.9 ± 124.9**	**1,314.2 ± 378.6**	**27**	**< 0.01**
Straightness index	0.80 ± 0.07	0.82 ± 0.01	11	0.727

duration, which resulted in faster daily travel speed in spring compared to that in autumn.

Discussion

The Bar-headed Goose is the only goose species to exploit the high plateau habitats of Asia, and our data are the first to confirm the prominent importance of the QTP to different elements of the Bar-headed Geese using the Mongolia–QTP–South Asia migration corridor. Despite the apparent existence of three discrete Bar-headed Goose sub-populations with different breeding and wintering grounds in this migration corridor, revealed by our tracking, they all showed a preference for exploiting the QTP at some time in their annual life cycle. The ToT geese completed their entire annual life cycle within the QTP. Compared with the parameters of TtoT geese described in Prosser *et al.* (2011), geese departed Qinghai Lake earlier in 2016 (26 August) than in 2007–2008 (13 October), used similar numbers of stopover sites (2.5 in 2016 and 2.1 in 2007–2008) but arrived at the Yarlung Zangbo River at a similar date (12 November 2016 and 8 November 2008 in 2007–2008). Possible reasons why the

2016 tagged geese departed so early include the fact that the rehabilitated birds had not reproduced that summer and that they may have accumulated sufficient fat stores for migration during the rescue period when maintained on a good diet. These individuals then spent longer at stopover sites before the ultimate drop in temperature pressed them onwards at a similar date to the birds tracked in 2007–2008. We are, however, prudent about concluding too much from so few likely atypical rehabilitated individuals, and urge further tracking to confirm these patterns. Excluding the *c.* 120 days travelling to Mongolia to breed (Wurdinger 2005), the MtoT geese completed the rest of their annual life cycle within the QTP. MtoA geese were present in the QTP for almost 116 days during autumn and spring migration, and departed their Mongolian breeding areas much earlier (1 September) than the sympatric Greylag Geese *Anser anser* (25 September; Li *et al.* 2020b) and Swan Geese *Anser cygnoides* (13 September; I. Damba, unpubl. data). This suggests that Bar-headed Geese are not forced out in autumn by low temperatures (the so-called "frost wave"; Xu & Si 2019) but the decision was driven by other factors, such as relative food quality along the flyway.

Both MtoA and MtoT geese caught on the breeding grounds in Mongolia spent a disproportionate amount of time on the QTP during migration. For example, MtoA geese spent 84% of their total migration duration there, while completing just 46% of their total migration distance on the QTP during autumn migration. Likewise, 86% of spring migration duration was spent on the QTP but it accounted for just 39% of the total distance. MtoT geese spent 98% of their total migration duration covering 63% of the total migration distance during autumn; this was apparently not the case in spring (53% of duration in 55% of distance), but the spring data originated from only a single individual. Within the QTP, MtoT geese had an average migration step length of 553 km, significantly longer than 356 km of the MtoA geese and 388 km of the TtoT geese, which explains why MtoT geese finished migration earlier than the other sub-populations. Outside of the QTP, MtoA and MtoT geese showed an average step length of 977 km and 1,058 km, and spent 8 days and 1 day completing their 2,519 km and 1,058 km (using no stopover sites outside of the QTP) migration distances, respectively. These are in sharp contrast with MtoA and MtoT geese migrating within the QTP (which used 72 days to cover 2,149 km and 45 days for 1,836 km, respectively). These observations confirm the significance of the QTP to the species, across three contrasting migration strategies adopted by the tagged birds followed in this investigation. In a recent review, Xu & Si (2019) showed that wetlands of various kinds covered 359,138 km^2 (3.8%) of mainland China's territory, of which the majority were situated in the QTP. The same authors showed that, unlike much of the rest of China, the extent of these wetlands had actually increased between 2000 and 2015. This may imply that not only do these wetlands within the QTP provide extensive suitable habitats that are of importance for waterbirds such as Bar-headed Geese in the East Asian Flyway, but their potential carrying capacity may be increasing.

The duration of autumn migration among MtoA tagged geese was 1.67 times longer than spring migration, the difference largely explained by extended periods spent at more stopover sites along the route during this season. Similar results were forthcoming among Western Flyway Bar-headed Geese (38–53 days migration duration in autumn; 18–30 in spring; Köppen *et al.* 2010), as well as sympatric Greylag Geese (53 days in autumn and 34 days in spring; Li *et al.* 2020b) and Swan Geese (64 days in autumn and 30 days in spring; I. Damba, unpubl. data) in eastern China. This contrasts with the general pattern of autumn migration duration among the geese and swans that breed in the arctic and winter in east Asia. For these species, autumn migration duration is generally shorter than in spring, as among Greater White-fronted Geese *Anser albifrons* (35 days in autumn and 79 days in spring; Deng *et al.* 2019) and Bewick's Swans *Cygnus columbianus bewickii* (55 days in autumn and 76 days in spring; Huang *et al.* 2018). The difference in migration duration between geese and swan species breeding in the Mongolian Plateau and those breeding in the east Russian arctic may be caused by the sequence of temperature changes they encounter along their migration routes. In spring, despite the higher altitude, grass growth phenology on the Mongolian Plateau commences at a considerably earlier date than at high latitudes in the arctic. Not only does this ensure an earlier start, but birds breeding in the arctic encounter highly variable patterns of snow melt along their migration corridors, which can slow northbound progress unpredictably. Late snow melt may also impose long waiting times at ultimate breeding sites (which may expose arctic-nesting geese to periods of low food availability and high predation pressure) whilst the nesting territories become free of snow (Kölzsch *et al.* 2016; Li *et al.* 2020a). In autumn, arctic geese and swans start migration later in order to accumulate more energy stores from the pulse of summer production. Due to the frost wave (Xu & Si 2019), they arrive to the wintering grounds quickly to occupy wintering habitats early and to replenish the energy expended along the long-distance and large-step length migration (Wang *et al.* 2018). In contrast, the geese that breed at the Mongolian Plateau migrate in smaller step lengths, for reasons we do not fully understand, which should be the subject of further investigation.

As a result of climate change, wetlands within the QTP are currently expanding mainly along the Mongolia–QTP–South Asia migration corridor, but have also begun to contract in the western QTP (mainly in Ngari Prefecture, China) over the past 15 years (Xu *et al.* 2019). Because the Bar-headed Geese prefer to select wetlands as habitat throughout the entire annual life cycle (Yang *et al.* 2013; Zheng *et al.* 2018; Zhang *et al.* 2020), the geese passing through the eastern QTP have benefitted from the continued (and possibly increased) availability of natural wetland feeding areas in this migration corridor. The species has also benefitted from the increase in the area of farmland on the wintering grounds in Shigatse Prefecture and have been seen to shift increasingly to agricultural feeding. For instance, numbers of Bar-headed Geese wintering along the Yarlung Zangbo River in the eastern QTP rose from 15,000 in the 1990s (Bishop *et al.* 1997) to 30,000 in 2007 (Bishop & Tsamchu 2007) then 67,000 in 2014 (Liu *et al.* 2017), and this is partly attributable to their change in feeding habitat. In contrast, the contraction in wetland area in the western QTP may have led to a deterioration in feeding conditions for Bar-headed Geese, which annually use this migration corridor. This underlines the need for tracking studies such as this one for determining the sub-population structure of such migrant species, in order to understand their precise conservation needs and pressures throughout the annual cycle better than we do at present. In this case, we particularly urge more deployment of telemetry devices to confirm these patterns and contribute to our knowledge of migration routes and key stopover sites, in combination with ground surveys of the QTP staging areas, to identify potential threats to staging areas used by different sub-populations in the Eastern Flyway. It is clear that the differential effects of climate change on the hydrology of QTP wetlands will disproportionally affect different sub-populations synchronously, so we need this knowledge rapidly if we are to be successful in achieving effective protection for all of the sub-populations using the QTP as key staging and wintering areas.

Acknowledgements

We gratefully acknowledge the contributions of Xin Wang, Xianghuang Li and Hongbin Li for their help on data analysis. This study was supported by the National Natural Science Foundation of China (Grant Nos. 31870369, 31970433 & 31670424) and China Biodiversity Observation Networks (Sino BON). We thank The Animal Ethics Committee, Research for Eco-Environmental Sciences, Chinese Academy of Sciences for approving this study and the Qinghai Lake National Nature Reserve authorities for transmitter deployment permits at Qinghai Lake, China. We are also grateful to the Ministry of Nature, Environmental and Tourism of Mongolia for granting capture and sampling permits in Mongolia and the Wildlife Science and Conservation Center of Mongolia. Two anonymous referees made helpful comments on the manuscript.

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