

Geographic variation in Bar-headed Geese *Anser indicus*: connectivity of wintering areas and breeding grounds across a broad front

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Abstract

The connectivity and frequency of exchange between sub-populations of migratory birds is integral to understanding population dynamics over the entire species' range. True geese are highly philopatric and acquire lifetime mates during the winter, suggesting that the number of distinct sub-populations may be related to the number of distinct wintering areas. In the Bar-headed Goose *Anser indicus*, a species found exclusively in Central Asia, the connectivity between breeding and wintering areas is not well known. Their migration includes crossing a broad front of the Himalaya Cordillera, a significant barrier to migration for most birds. Many Bar-headed Geese fly to breeding areas on the Tibetan-Qinghai Plateau (TQP), the highest plateau in the world. From 2005–2008, 60 Bar-headed Geese were captured and marked with satellite transmitters in Nepal ($n = 2$), India ($n = 6$), China ($n = 29$), and Mongolia ($n = 23$) to examine their migration and distribution. Distinct differences were observed in their migration corridors and timing of movements, including an apparent leap-frog migration pattern for geese from Mongolia. Measurements of geese from Mongolia were larger than their counterparts from China, providing some evidence of morphological differences. Alteration of habitats in China, including the warming effects of climate change on glaciers increasing runoff to TQP wetlands, may be changing goose migration patterns and timing. With the exception of one individual, all geese from Qinghai Lake, China wintered in the southern TQP near Lhasa, and their increasing numbers in that region may be related to the effects of climate change and agricultural development. Thus, our findings document both morphological and geographical variation in sub-populations of Bar-headed Geese, but their resilience to environmental change may be lost if migratory short-stopping results in larger congregations restricted to a smaller number of wintering areas.

Key words: Anserini, Central Asian Flyway, Himalaya, migration, satellite telemetry.

Delineation of discrete sub-populations of species is a critical step towards conserving geographically distinct morphological, behavioural, and ecological traits (Moritz 1994), which are often necessary precursors

for species evolution (Endler 1977; Zink 1989). Defining sub-populations based on geographic variation for migratory species has proven challenging due to variable rates of gene flow among highly mobile species

(Syroechkovsky *et al.* 1994) and difficulties in linking genetic variation with behavioural and demographic variation within populations (Bensch *et al.* 1999; Paetkau 1999; Lovette *et al.* 2004; Iverson & Esler 2006). For waterfowl, the wintering areas, migration pathways, and breeding grounds of many species are poorly known (Ely & Takekawa 1996), and identifying these for sub-populations, as well as the strength of migratory connectivity and frequency of exchange between population segments, is integral to understanding population dynamics over a species' annual cycle (Syroechkovsky *et al.* 1994; Esler 2000; Webster *et al.* 2002; Iverson & Esler 2006). Identifying geographic variation among sub-populations of migratory species allows for the designation of management units (Moritz 1994) on a smaller scale than could otherwise be determined (Milot *et al.* 2000) and results in more effective conservation strategies.

Geese (tribe Anserini) are long-lived, and unlike most avian species, exhibit male-biased dispersal and female philopatry (Robertson & Cooke 1999). Mate choice often does not occur on the breeding ground, but during winter or the spring migration, and often results in permanent pair bonds (Ganter *et al.* 2005). If numerous breeding populations share wintering sites during the non-breeding season, or demonstrate weak migratory connectivity, gene flow is expected to be high because mated males will follow the females to their natal nesting sites (Avisé *et al.* 1992; Ely & Scribner 1994). Conversely, if wintering areas and migratory flyways of breeding populations are spatially or temporally

isolated, there would be limited exchange of individuals and demographically independent sub-populations could arise (Esler 2000; Ruokonen *et al.* 2000). Individuals of segregated sub-populations may develop behavioural and morphological adaptations unique to their specific wintering or breeding habitats and migration pathway (Webster *et al.* 2002), as well as local knowledge of patchy food resources and refuges (Robertson & Cooke 1999). As a result, sub-populations may merit unique conservation designation and management in order to preserve biologically relevant traits (*e.g.* Whooping Cranes *Grus americana* in North America; Glenn *et al.* 1999).

The Bar-headed Goose *Anser indicus* is a monotypic species with a global population of < 60,000 individuals in the wild (Miyabayashi & Mundkur 1999, updated in 2005). Bar-headed Geese breed in selected wetlands on the high plateaus of central Asia (Fig. 1a), exhibiting a discontinuous breeding range across a broad front extending more than 3,500 km from Kyrgyzstan to central China, and as far north as Mongolia (Wurdinger 2005). More than 25% of the world population winters on the southern Tibetan-Qinghai Plateau (TQP; Bishop *et al.* 1997), while India is a winter terminus for another 25–50% of the population (Fig. 1b; Javed *et al.* 2000). The Himalayan Cordillera presents a formidable barrier to avian migration (Miyabayashi & Mundkur 1999; Javed *et al.* 2000; Johansson *et al.* 2007), as the majority of passes through the Himalayas are > 5,000 m above sea level. Bar-headed Geese are believed to be one of the highest flying birds and



Figure 1. Summary of reported (a) breeding and (b) wintering locations for Bar-headed Geese (adapted from Miyabayashi & Mundkur 1999). Relative numbers of wintering geese are indicated by the size of the circle.

possess unique physiological traits adapted for sustaining flight at high altitude (Ward *et al.* 2002; Scott & Milsom 2007; Lee *et al.* 2008). Individuals marked with satellite transmitters have been confirmed to fly over the Himalayas (Javed *et al.* 2000), and geese have been observed flying over Mount Everest (> 9,000 m; Swan 1970). However, few empirical data exist about the migration ecology of Bar-headed Geese and the specific pathways used to cross the Himalayas. If different routes are commonly used by different segments of the population, the Himalayas may serve as a coarse filter that would contribute to the formation of geographic sub-populations.

Bar-headed Geese may be vulnerable to population declines as a result of wetland loss in over-wintering areas (Foote *et al.* 1996), severe climate change-induced habitat alteration on portions of their breeding range (Wang *et al.* 2008; Xu *et al.* 2008), hunting pressure (Green 1992; Gole 1997), and susceptibility to emerging infectious diseases such as highly pathogenic avian influenza H5N1 (Chen *et al.* 2005; Brown *et al.* 2008). Determining if geographic variation occurs in migratory movements of the Bar-headed Goose will contribute to identifying appropriate management strategies to conserve unique population segments. Here, we present results for Bar-headed Geese marked with satellite transmitters from four different countries in the Central Asian Flyway. Their migration ecology is described, and this example is used to review implications of geographic variation among sub-populations.

Methods

Capture sites

Bar-headed Geese were captured in China, India, Mongolia, and Nepal. The specific areas included: 1) China (Fig. 2a) – Qinghai Lake National Nature Reserve (36°49'N, 99°49'E) is located in the northeast of TQP, 280 km west of Xining in Qinghai Province (Liu *et al.* 2004). Qinghai Lake is the largest (526 km²) saltwater lake in China at an elevation of 3,193 m. It is an important migration area for waterbirds in the Central Asian Flyway as well as the world's largest known breeding area for Bar-headed Geese; 2) India (Fig. 2b) – Keoladeo National Park (27°9'N, 77°30'E) is west of Bharatpur in the state of Rajasthan, 50 km west of Agra and 178 km northeast of Jaipur (Gopal 1994). The 29 km² area was originally developed as a waterbird area for hunting in 1899 by the Majoraja of Bharatpur (Vijayan 1988). A man-made wetland in the floodplain of the Gambhir and Banganga River, inundation occurs during October, drops through the winter and then quickly dries from March through June (Middleton 1989); 3) Mongolia (Fig. 2c) – Terkhiin Tsagaan Lake (48°8'N, 99°38'E) is a freshwater body situated within a 77,267 ha national park at high altitude in the Khangai mountainous regions of Taryat Soum in Arkhangai Aimag, central Mongolia; and 4) Nepal (Fig. 2d) – Chitwan National Park (27°30'N, 84°30'E) is the oldest national park in Nepal, located 10 km west of Bharatpur in the sub-tropical Terai lowlands of southcentral Nepal. The 932 km² area is bisected by floodplains of the Narayani

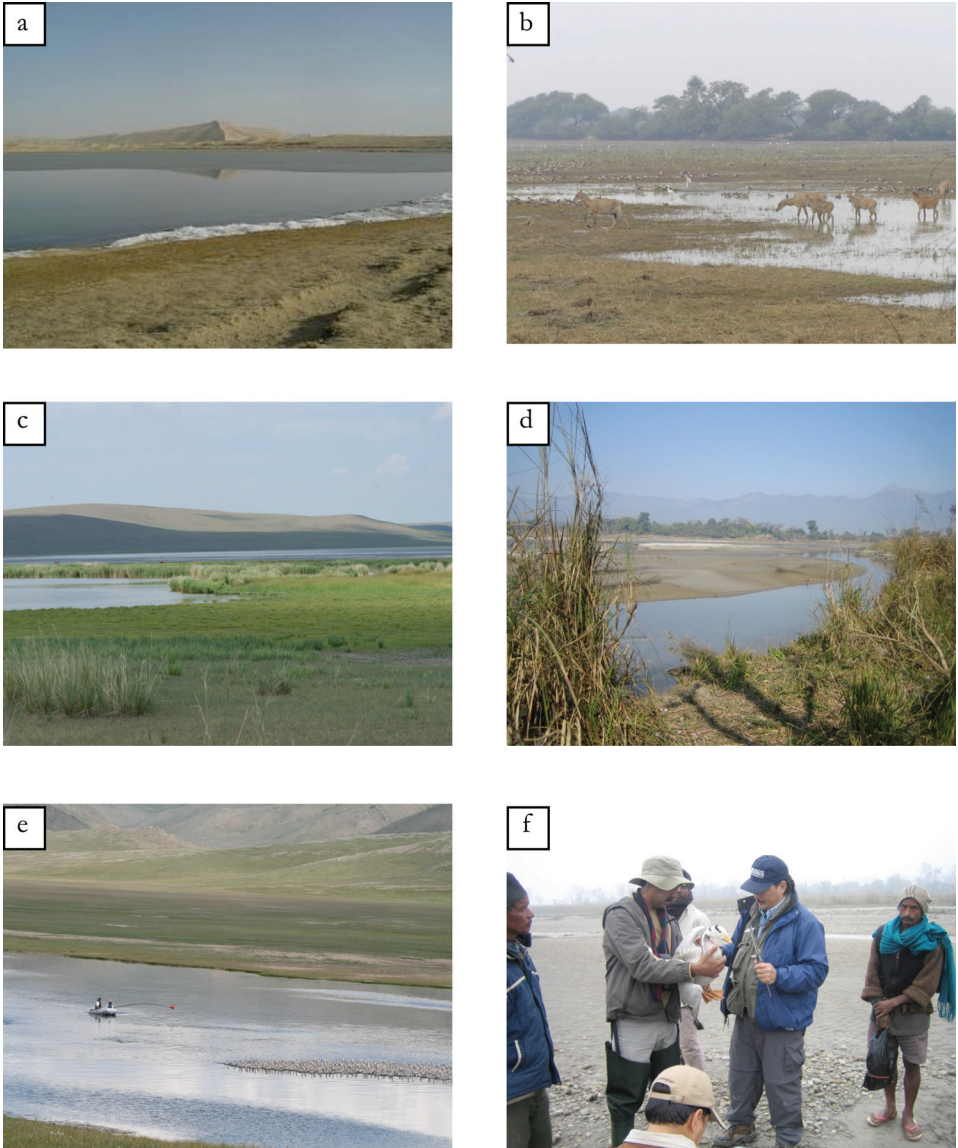


Figure 2. Capture and marking of Bar-headed Geese took place in four countries: (a) Qinghai Lake in China (breeding grounds); (b) Keoladeo National Park in India (wintering area); (c) Terkhiin Tsagaan Lake in Mongolia (moulting site); (d) Chitwan National Park in Nepal (wintering area); and (e) drive-trap captures in Mongolia; and (f) recording measurements in Nepal.

River and provides habitat for more than 450 species of birds.

Capture and marking

A total of 60 individuals were caught and marked at Qinghai Lake (March 2007 and September 2007, $n = 29$), Keoladeo Ghana (February 2005, $n = 6$), Royal Chitwan (February 2005, $n = 2$), and Terkhiin Tsagaan Lake (July 2008, $n = 23$). Geese were captured with leg nooses consisting of monofilament loops attached to wooden sticks connected with nylon cord in lines of 50–100 nooses, or they were captured during the moult by herding them into a drive-trap (Fig. 2e). Upon capture, geese were immediately removed, placed in individual cloth bags, and processed to record sex, age, weight, mass, flat wing, and diagonal tarsus (Fig. 2f). Selected individuals were marked with 30–70 g battery or solar-powered Platform Terminal Transmitters (PTTs: Microwave Telemetry, Inc., Columbia, MD, USA) attached with Teflon harnesses (Bally Ribbon Mills, Bally, PA, USA) or glued to plastic neck collars (three in India, one in Nepal). Transmitter packages weighed 2.1–3.0% of the goose's body mass. Geese were released as close to capture locations as possible, typically within 1–4 h of capture. Procedures for capture, handling, and marking were reviewed and approved by the Animal Care and Use Committee of the USGS Western Ecological or Patuxent Wildlife Research Centers and the University of Maryland, Baltimore County (Protocol EE070200710).

Tracking and analysis

Transmitters were programmed to obtain locations for 6 h each 2–3 days (Argos

PTTs) while GPS transmitters logged 12–24 locations each day, and data were uploaded every second day to the Argos satellite tracking system (CLS America Inc., Largo, MD, USA). Data were recovered via receivers aboard polar-orbiting weather satellites. CLS calculated PTT locations from the perceived Doppler-effect shifts in transmission frequency during a satellite overpass. The accuracy of each Doppler-derived location was rated by CLS and assigned a location class index. Standard and conventional location classes 0, 1, 2, and 3 indicated that the location was derived from ≥ 4 transmissions and possess 1-sigma error radii with accuracy of $> 1,000$ m, 350–1,000 m, 150–350 m, and ≤ 150 m, respectively. CLS does not attribute accuracy estimates for the auxiliary location classes A (3 transmissions) and B (2 transmissions). Transmitters from 2005 in India and Nepal were programmed to turn off in mid-December because of sponsor funding limitations.

ArcGIS 9.2 (Environmental Systems Research Institute, Inc., Redlands, California, USA) and Google Earth 5.0 (Google, Mountain View, California, USA) were used to plot and analyse the telemetry locations. The Doppler-derived location data were compiled and validated with the Douglas-Argos Filter Algorithm (D. Douglas, Version 7.03, <http://alaska.usgs.gov/science/biology/spatial/>). The filtering algorithm identified and removed implausible auxiliary Doppler locations based on distance moved, movement rate, and turning angle between each previous and subsequent location.

The spatial extent of migration was characterised for each sub-population by

creating minimum convex polygons through Animal Movement Extension (Hooge & Eichenlaub 1997). In this case, the minimum convex polygons were not used to represent individual home ranges or to compare area statistics. Instead, they were used as a simple method to visually group individuals together from the same sub-populations, and we smoothed the outline around areas without locations to create a better depiction of the geographic distribution from the satellite telemetry locations. Two-way analysis of variance tests were applied by age and sex to examine differences in the morphometrics of the geese from the Qinghai Lake and Terkhiin Tsagaan Lake sub-populations where the sample size was sufficient.

Results

Geographic variation

A total of 93,009 locations were obtained from the 60 satellite-marked Bar-headed Geese, with an average of 1,550 locations from each individual. All of the marked geese migrated within the Central Asian Flyway (Table 1), and their northernmost extent of migration was to west-central Mongolia (Prosser *et al.* 2009). The general movement patterns of individuals within each sub-population were similar, while the overall migration routes between sub-populations differed (Fig. 3).

China. In total, 52,971 locations were obtained from March 2007 through January 2009 for the 29 Bar-headed Geese marked at Qinghai Lake in the spring and fall of 2007 and 2008. These included 41,189 (77.8%) GPS locations and 11,782 (22.2%) Argos

locations, including 3,102 (26.4%) class 1–3 locations. Total numbers of Bar-headed Geese at Qinghai Lake exceed 10,000 individuals. Many geese moved south to post-breeding areas for moult (Table 1) from 20 June (range 9 June–2 July) to 7 September (21 August–10 September). This included a concentration of geese in the Maduo region of Qinghai Province, 300 km southwest of Qinghai Lake where several geese spent more than a month. Geese departed from Qinghai Lake during two time periods, likely representing: (1) non-breeding geese moving to moulting areas during the early phase, and (2) geese that attempted to breed departing at the later phase. After a period of up to 3 months in these areas, the geese commenced their fall migration in mid October and arrived at their wintering area near Lhasa in the southern TQP on 29 October to 9 December. Only one individual in the 2 years of study crossed the Himalaya and flew to the east coast of India near Satabhaya, Orissa State at the mouth of the Baltarani River on 9 December 2008 (Fig. 3). The wintering geese commenced their spring migration northwards between 7 March and 24 April. They arrived in the breeding area on the Qinghai Plateau from late March to early May, and they remained at the breeding grounds through mid June. Geese from this sub-population flew an average of 1,100 km from their wintering areas (29°30'N; 4,000 m elevation) to their breeding grounds (37°0'N; 3,200 m elevation).

India. In total, 10,020 locations were obtained for the six Bar-headed Geese marked at Keoladeo in the winter of 2005,

Table 1. Chronology of spring migration, breeding, post-breeding, fall migration, and wintering periods for Bar-headed Geese marked with satellite transmitters from four sub-populations: China ($n = 29$), India ($n = 6$), Mongolia ($n = 23$), and Nepal ($n = 2$). The number of geese used to estimate mean departure and arrival dates (date range in parentheses), and the number of days for each stage of the annual cycle (based on the estimated mean departure and arrival dates) are reported for each period.

Sub-population	Spring migration			Breeding area			Post-breeding area (moult)			Fall migration			Wintering area		
	<i>n</i>	Departure	Days	<i>n</i>	Arrival	Days	<i>n</i>	Arrival	Days	<i>n</i>	Departure	Days	<i>n</i>	Arrival	Days
China*	10	31 Mar (7 Mar–24 Apr)	20	7	22 Apr (27 Mar–10 May)	75	21	7 Jul (10 Jun–3 Jul)	101	22	16 Oct (29 Sep–29 Oct)	23	17	8 Nov (29 Oct–9 Dec)	142
India**	5	10 Apr (27 Mar–18 Apr)	1	5	11 Apr (28 Mar–19 Apr)	213	1	9 Jul (–)	154	3	10 Nov (1 Nov–20 Nov)	8	2	18 Nov (16 Nov–21 Nov)	143
Mongolia	1	29 Mar (–)	–	–	– (–)	–	–	– (–)	–	19	8 Sep (26 Aug–20 Sep)	78	8	25 Nov (26 Oct–15 Dec)	124
Nepal*	2	20 Mar (14 Mar–27 Mar)	34	2	23 Apr (16 April–1 May)	107	2	8 Aug (15 Jun–1 Oct)	114	2	30 Nov (25 Nov–5 Dec)	1	2	1 Dec (26 Nov–6 Dec)	108

*Bimodal arrival at post-breeding moult sites (early and late)

**One bird likely nested and failed in mid-April, then possibly attempted re-nesting in May before moving to a moulting area

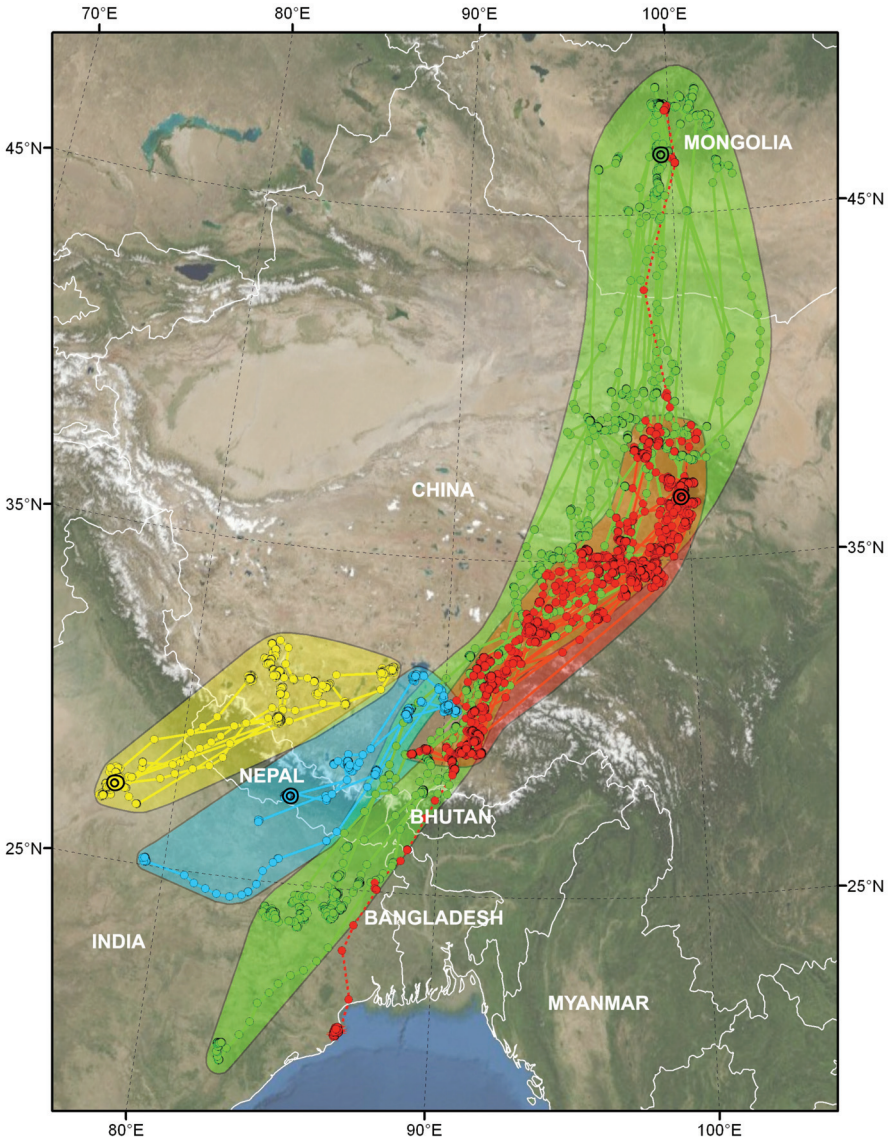


Figure 3. Locations (circles), migration pathways (lines), and capture areas (rings: see Capture sites for detailed description) for 60 Bar-headed Geese marked with satellite transmitters in China (red), India (yellow), Mongolia (green), and Nepal (blue). Representation of each sub-population was depicted with a 95% minimum convex polygon smoothed to remove areas without locations. The Himalayas are highlighted in white. The red-dotted line between China and Mongolia represents a goose marked pre-breeding (April) at Qinghai Lake, China, which migrated to Mongolia for breeding; all other red lines represent birds marked post-breeding at Qinghai Lake.

although we lost signals from one PTT shortly after deployment. These locations included 9,099 (90.8%) GPS locations and 921 (9.2%) Argos locations, including 554 (60.2%) class 1–3 locations. Numbers of Bar-headed Geese at Keoladeo were estimated at 1,500 to 2,000 geese. The geese departed from Keoladeo between 27 March and 18 April (mean 10 April) and soon thereafter, crossed the Himalayas in a single day (Table 1). Individuals arrived at breeding grounds on the TQP from 28 March to 19 April (mean = 11 April). One goose used the very same wetland as did the first Bar-headed Goose marked with a satellite transmitter five years earlier (Javed *et al.* 2000). The geese moved from river valleys to breeding lakes following the spring thaw. Signals from three PTTs ceased during the breeding season, but the remaining two birds initiated fall migration on 10 November and arrived back to wintering areas from 16–21 November (mean = 18 November) before their transmitters were programmed to turn-off in mid December. Geese from this sub-population flew an average of 800 km from wintering areas (27°30'N; 200 m elevation) to their breeding grounds (31°0'N; 4,800 m elevation).

Mongolia. In total, 22,239 locations were obtained for 23 Bar-headed Geese marked at Terkhiin Tsagaan Lake through January 2009. These included 17,341 (78.0%) GPS locations and 4,898 (22.2%) Argos locations, including 1,170 (23.9%) class 1–3 locations. In the vicinity of the lake, we estimated as many as 3,000 Bar-headed Geese. Fall migration was initiated from 26 August to 20 September (mean = 8

September; Table 1) and arrived at wintering areas in the Bihar and States of northeast India (Fig. 3) from 26 October–15 December (mean = 25 November). At least four Bar-headed Geese marked at Terkhiin Tsagaan Lake did not cross the Himalayas and instead over-wintered in Qinghai Province ($n = 2$) or the Tibetan Autonomous regions ($n = 2$) of the TQP. The spring migration was initiated on 29 March. Geese from this sub-population flew 3,000 km from wintering areas (22°30'N; 150 m elevation) to their breeding grounds (47°30'N; 2,100 m elevation).

Nepal. In total, 7,779 locations were obtained for the two Bar-headed Geese marked at Chitwan in January and February 2005. The small wintering population was estimated to be about 200–300 individuals. Tracking data were comprised of 7,240 (93.1%) GPS locations and 539 (6.9%) Argos locations, including 310 (74.4%) class 1–3 locations. The geese initiated spring migration from 14–27 March and crossed the Himalaya to the TQP in a single day (Table 1). They arrived at breeding areas by 23 April where they remained for 3 months. They moved to post-breeding areas for moult from 15 June–1 October, and they commenced their fall migration on 30 November, arriving at their wintering area in north central India between 26 November and 6 December. After their transmitters turned off in mid December, one individual was observed to the south of Nepal on the Ganges River plain of India in early January. Geese from this sub-population flew 500 km from wintering (27°30'N; 150 m elevation) to breeding areas (31°0'N; 5,000 m elevation).

Morphological variation

Analysis was performed for uncorrected body mass, culmen, and diagonal tarsus of male and female Bar-headed Geese (Fig. 4) from the China and Mongolia sub-populations where sample numbers were adequate for comparison. Measurements were not adjusted for sampling bias related to differences in sample periods, but culmen and tarsus measurements were unlikely to be biased since they do not change seasonally in adult birds. The interactions of sub-population and sex were confounded for both mass ($F_{1,98} = 16.6$, $P < 0.001$) and culmen ($F_{1,100} = 85.1$, $P < 0.001$). Males caught in the spring and the fall in China were heavier than Mongolian males caught in the late summer, while Mongolia females caught in the late summer were heavier than late summer females in China. Although the culmen of females from Mongolia were larger than those from China, the males had similar-sized culmens. However, tarsi were significantly larger for individuals from the Mongolian sub-population for both sexes ($F_{1,100} = 85.1$, $P < 0.001$).

Discussion

Geographic variation and intra-specific diversity

Distinct differences emerged in the wintering and breeding distribution of Bar-headed Geese marked across their range. Based on the migration pathways, we propose the existence of at least three sub-populations of Bar-headed Geese characterised by their primary use of distinct wintering areas and breeding grounds: India–Nepal, China, and Mongolia.

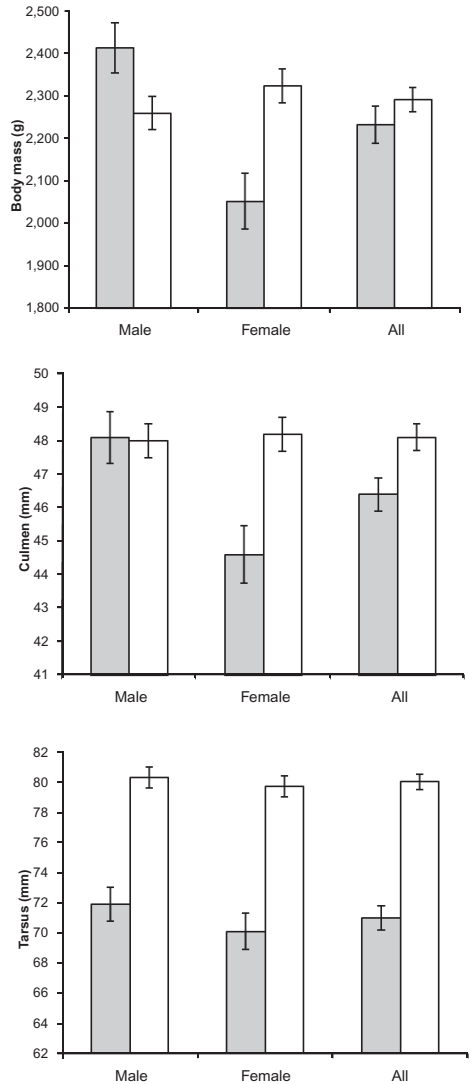


Figure 4. Differences in mean (\pm s.e.) unadjusted body mass, culmen, and diagonal tarsus measurements of adult male and female Bar-headed Geese captured at Qinghai Lake National Nature Reserve, China in April and September 2007 (shaded bars: 16 males, 13 females), and Terkhiin Tsagaan Lake, Mongolia in July 2008 (unshaded bars: 38 males, 35 females).

Geese captured at wintering areas in India–Nepal migrated short distances of 500–800 km from their wintering areas on the Indian subcontinent to breeding grounds in the southern TQP near Lhasa, but ascended more than 4,500 m in elevation. Geese captured in China migrated 400–800 km farther than geese from India–Nepal from their wintering areas to their breeding grounds on the TQP, but their breeding and winter areas were both at high elevation varying by only 800 m (wintering area, 4,000 m; breeding grounds 3,200 m). Finally, geese captured in Mongolia demonstrated a leap-frog migration (Salomonsen 1955) over the other sub-populations, flying 3,000 km from wintering areas on the Indian subcontinent 700 km south of geese from China to breeding grounds in Mongolia 1,200 km farther north.

Variation among sub-populations is of critical importance for a species to be resilient to environmental change, demographic stochasticity, and disease (Keller & Waller 2002; Jamieson *et al.* 2008). Sub-populations may possess behavioural, morphological, and physiological adaptations unique to their specific wintering and breeding habitats and migration pathways (Webster *et al.* 2002). These may reduce the vulnerability of the species as a whole to extreme environmental fluctuations. Data from numerous taxa have demonstrated that lowered variation is correlated with reduced population growth (Keller & Waller 2002), so the preservation of genetic diversity is now recognised as a key component in the development of management strategies for threatened populations around the world (Amos & Balmford 2001).

Sub-populations may arise because of the effects of any number of behavioural, geographic, or demographic factors (Grant & Grant 1987; Grant & Grant 2003). Migratory species like Bar-headed Geese with high levels of philopatry to both wintering and breeding grounds are more likely to have demographically independent sub-populations because of limited exchange of individuals across population segments (Esler 2000). Low rates of dispersal within populations may homogenise sub-populations genetically (Slatkin 1985), but fine-scale genetic relatedness among neighbouring nest clusters has been documented in migratory ducks (McKinnon *et al.* 2006; Waldeck *et al.* 2008) and geese (Fowler *et al.* 2005; Lecomte *et al.* 2009). Non-random dispersal may reinforce evolutionary differentiation at fine spatial scales (Garant *et al.* 2005) even if gene flow is occurring (Lecomte *et al.* 2009).

We suspect that because the migration of the Bar-headed Goose extends across a broad front (Miyabayashi & Mundkur 1999; Javed *et al.* 2000), they may have several distinct sub-populations. Greater White-fronted Goose *Anser albifrons* sub-populations exhibited breeding allopatry and temporal partitioning on staging and wintering areas across their Holarctic distribution. They may represent a group of sub-species connected by clines (Ely & Takekawa 1996) which also may be true of Bar-headed Geese at a smaller scale. Use of different migratory flyways contributed to partitioning of genetic variation for some species of ducks (Gay *et al.* 2004; Peters *et al.* 2005), but not in others (Cronin *et al.* 1996;

Pearce *et al.* 2004; Peters & Omland 2007). The monogamous behaviour of geese that typically pair on their wintering areas (Robertson & Cooke 1999) may sustain higher differentiation among their sub-populations.

Leap-frog migration and clinal variation

Although leap-frog migrations have been discussed for many passerine species (Kelly *et al.* 2002; Paxton *et al.* 2007) they have not been frequently reported for migratory geese (except Greylag Geese *Anser anser*, Madsen *et al.* 1999). Leap-frog migration may occur depending on the cost of spring migration in relation to its timing and the risks of the route taken (Bell 1997). Bar-headed Geese are characterised by small wintering flocks of up to a few thousand individuals, although they often nest colonially (Owen 1980). Detrimental effects (*i.e.* mortality or reduced condition) for individuals that occupy wintering areas with harsh climatic conditions nearer to breeding grounds may be offset by earlier arrival to breed (Bell 1997); thus, the migration strategy employed by Bar-headed Geese in China wintering on the southern TQP may be offset by the short distance to their breeding colony. Migratory routes may be selected based on survival during migration versus survival through the wintering period (Bell 1997).

Two (India–Nepal and Mongolia) of the three sub-populations that were studied migrated over the Himalaya, an ecological barrier to migration (Javed *et al.* 2000; Gill *et al.* 2009) that may have played a prominent role in the diversification of population segments. Bar-headed Geese that cross the

Himalayas during migration may have different survival rates than those that do not fly over, resulting in distinct migration strategies. Mortality during migration may be much higher than during other parts of the annual cycle (Silllett *et al.* 2000), so selection should favour behaviours that minimise these risks (Hedenstrom 2008; Gill *et al.* 2009). Migration over the Himalayas represents an immense physiological challenge (Ward *et al.* 2002; Scott & Milsom 2007; Lee *et al.* 2008), and one which may result in intense natural selection towards localised behavioural and phenotypic adaptations specific to each migration pathway.

We assumed that the behaviour of our radio-marked sample was representative of the sub-populations from which they were derived. However, not all geese from the different sub-populations showed similar movements. Some geese ($n = 4$) marked in Mongolia were confirmed to over-winter in the southern TQP, one goose marked at Qinghai Lake in the spring (April) migrated north to Mongolia (Prosser *et al.*, 2009), and one goose from Qinghai Lake migrated to northern India during the winter. Consistent with this finding, only three of 22 indirect recoveries were reported south of China from 802 Bar-headed Geese banded at Qinghai Lake from 1983–1985 (Lu 1997), and several Bar-headed Geese marked recently with collars in central Mongolia during the summer have been sighted in India (T. Mundkur, pers. comm.). In addition, several of the marked geese from Mongolia migrated through Bhutan, northeast India, and Assam, an area where Bar-headed Geese are reported to

commonly occur during the migration and in the winter (Choudhury 1997).

Goose populations that span the Northern Hemisphere such as the Greater White-fronted Goose show clinal variation in morphology (Ely *et al.* 2005). Even across a smaller geographic range, morphological measurements indicated that Bar-headed Geese from Mongolia had larger tarsi than geese from China, and females had larger culmens. These morphological differences were similar to other studies where the leap-frogged population consisted of smaller individuals (Salomonsen 1955; Alerstam & Högstedt 1985). The morphological differences may be a unique example of Bergmann's rule (1847) among Bar-headed Geese, where populations that breed farther north are larger in size. However, the geese in China stay at higher altitudes throughout the year, which might have an environmental effect similar to that of geese migrating farther north. When compared with geese at low altitudes, Bar-headed Geese have the largest wing-span and smallest wing loading, but their flight morphology was found to be similar (Lee *et al.* 2008, Scott & Milsom 2007).

Bar-headed Geese are renowned for their migration across the Himalayas (Swan 1970; Javed *et al.* 2000), and they are physiologically adapted for flying at high altitude (Faraci *et al.* 1984; Faraci *et al.* 1985; Ward *et al.* 2002; Scott & Milsom 2007). Our studies of sub-populations show that some of the individuals never cross over the Himalayas and remain at high altitude (> 3,200 m) for the entire year. It is surprising that these geese persist through the winter at such high altitudes, but their wintering

success in the Lhasa Valley and adjacent areas may be related to their ability to find food in the region's agricultural fields, rather than their inability to survive in cold temperatures.

Short-stopping and changing wintering habitats

In waterfowl, there is evidence of both "short-stopping", where groups winter farther north than normal when habitat conditions are favourable (Hestbeck *et al.* 1991) and "over-flying", where groups breed in more northern locations when local conditions vary annually (Johnson & Grier 1988; Miller *et al.* 2005). Surveys conducted in the Lhasa, Brahmaputra and Nyang River Valleys have shown an apparent increase in numbers of Bar-headed Geese wintering in the southern TQP. Surveys in the early 1990s indicated about 3,000 wintering Bar-headed Geese in the Lhasa watershed and 13,000–14,500 individuals in the overall region (Bishop *et al.* 1997; Lang *et al.* 2007). More recent surveys estimated 6,000 individuals in the Lhasa watershed in 2000–2001 (Lang *et al.* 2007), and 31,955 individuals wintering in the overall region in 2006 (Bishop & Tsamchu 2007).

The increasing size of this sub-population or larger numbers short-stopping in the region may be a result of establishment of a new nature reserve in 2003 (Bishop & Tsamchu 2007), as well as agricultural development within the region. Changes in wintering foods may have resulted in population growth, or in short-stopping of migrating geese that formerly crossed into India. The change in wintering

distribution where the southern migration distance is shortened over time also has been observed in Lesser Snow Geese in North America (Alisauskas 1998). Changes in wintering location in waterfowl species have been associated with changes in refuge and food availability (Abraham & Jefferies 1997; Hill & Frederick 1997), population size (Alisauskas 1998), or temperatures (Hestbeck *et al.* 1991). In Greater Snow Geese, distributional shifts may be related to the greater availability of corn fields in mid-Atlantic flyway states than farther south in recent decades and to increasing temperatures throughout the wintering grounds (Gauthier *et al.* 2004). Development of modern agriculture may improve the condition of geese as they arrive on their breeding grounds (Krapu *et al.* 1995), leading to population growth (van Eerden *et al.* 2005).

Climate change and habitat loss

The strength of migratory connectivity among sub-populations will influence the ability of migratory species to adapt to changing environmental conditions resulting from climate change (Webster *et al.* 2002). If connectivity among the Bar-headed Geese sub-populations is strong, then individuals within each sub-population have been subjected to similar selective pressures in both wintering and breeding locations. This may have resulted in local adaptation that could limit response to large-scale climate change (Webster *et al.* 2002). For migratory birds, the timing of arrival on breeding territories and overwintering grounds is a key determinant of reproductive success, survivorship, and

fitness (Cotton 2003; Arzel *et al.* 2006; Laaksonen *et al.* 2006; Ely *et al.* 2007). Migratory species time their spring arrival to breeding grounds to coincide with peaks in food abundance, including the chick-rearing period (Arzel *et al.* 2009), and climate change patterns can result in mistimed migrations that lower breeding success and decrease population size (Both *et al.* 2006). Global climate fluctuations have been demonstrated to affect adult survival and fecundity (Sillert *et al.* 2000; Boyd & Fox 2008), and there is growing evidence that the timing of avian migration is affected by climatic change (Ahola *et al.* 2004; Both & te Marvelde 2007; Macmynowski *et al.* 2007; Parmesan 2007; Saino & Ambrosini 2008; van Buskirk *et al.* 2009).

Climate-change related influences to TQP wetland habitats are predicted to be particularly dramatic (Xu *et al.* 2008; Ramanathan & Feng 2009). Annual temperatures have increased in parallel with warming over the Northern Hemisphere, and the rate of increase is positively correlated with elevation (Liu & Chen 2000; Holmes *et al.* 2009). In the northern regions warming trends have led to arid conditions and lowered rainfall, leading to drought and reduced vegetation (Xu *et al.* 2008). The southern region has experienced the opposite effect, including more humid weather and favourable conditions for vegetation (Xu *et al.* 2008). Species distributions are expected to shift to higher elevations and latitudes with climate change (Wilson *et al.* 2005); Bar-headed Geese may alter their breeding and wintering distributions throughout their range. Single-brooded species, like the Bar-headed Goose,

may be particularly sensitive to climate change if migration patterns become mistimed with periods of peak food availability during the breeding season (Jiguet *et al.* 2007), which has resulted in population decline in other species (Both *et al.* 2006). While reproductive chronology phenology may advance with climate change, high spring temperatures and extreme values during the summer extremes may decrease reproductive success to fledging (Dickey *et al.* 2008).

Changes in winter carrying capacity may lead to uneven effects on geographically defined breeding populations (Mills & Weir 2007), and Bar-headed Geese may be particularly susceptible to rapid demographic changes as their wintering areas differ greatly, and each are subject to unique ecological stressors. Species like Bar-headed Geese exhibiting “broad spatial and short temporal ecology” may be “among the best natural biotic indicators of present and future integrity of landscape and global processes” (Kelly & Hutto 2005). The spatial adaptability of Bar-headed Geese and other species that use wetlands on the TQP merit close examination in coming years to determine population response to changing habitat conditions. This region is equally sensitive to local anthropogenic land use, which can contribute to soil erosion, vegetation degradation, and land desertification (Wang *et al.* 2008; Holmes *et al.* 2009). Many arctic-breeding goose populations around the world have become increasingly dependent on agricultural habitats throughout their range (Fox *et al.* 2005; Jefferies & Drent 2006), adding an additional level of complexity to

their susceptibility to habitat loss and conversion.

Wetland loss and degradation in the Indian subcontinent is a concern (Foote *et al.* 1996) that could prove catastrophic, especially to small, highly site-faithful populations (Ely & Takekawa 1996). Conflicting water demands threaten the wetlands of Keoladeo National Park, and proposed development of a paper plant (R. Suwal, pers. comm.) may have a negative effect on the riverine habitats of Chitwan National Park.

Disease transmission

Finally, geographic variation in sub-populations may be critical for understanding transmission of diseases such as highly pathogenic avian influenza H5N1. Bar-headed Goose populations have proven highly susceptible to HPAI H5N1 (Brown *et al.* 2008), and they were the main victim in the largest wild bird outbreak at Qinghai Lake in 2005 (Chen *et al.* 2005; Liu *et al.* 2005). Wild bird outbreaks occurring in the southern TQP near Lhasa may be linked by the Bar-headed Geese migrating from Qinghai Lake, but our sub-population delineation suggests that direct connectivity to wintering areas in India and Russia (Webster *et al.* 2006) is not as likely. Potential transmission risks at both ends of the flyway (Pearce *et al.* in press) may be clarified by developing a better understanding of the sub-populations that are represented across a species range.

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