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Satellite telemetry reveals long-distance migration in the Asian great bustard *Otis tarda dybowskii*

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The range of the great bustard stretches 10 000 km across Eurasia, one of the largest ranges of any threatened species. While movement patterns of the western subspecies of great bustard are relatively well-understood, this is the first research to monitor the movements of the more endangered Asian subspecies of great bustard through telemetry and to link a breeding population of Asian great bustards to their wintering grounds. Using Argos/GPS platform transmitter terminals, we identified the annual movement patterns of three female great bustards captured at their breeding sites in northern Mongolia. The 4000 km round-trip migration we have recorded terminated at wintering grounds in Shaanxi, China. This route is twice as long as has previously been reported for great bustards, which are among the heaviest flying birds. The journey was accomplished in approximately two months each way, at ground velocities of 48–98 km h^{-1}, and incorporated multiple and variable stopover sites. On their wintering grounds these birds moved itinerantly across relatively large home ranges. Our findings confirm that migratory behavior in this species varies longitudinally. This variation may be attributable to longitudinal gradients in seasonality and severity of winter across Eurasia. The distance and duration of the migratory route taken by great bustards breeding in Mongolia, the crossing of an international border, the incorporation of many stopovers, and the use of a large wintering territory present challenges to the conservation of the Asian subspecies of great bustard in this rapidly changing part of the world.

The range of the great bustard *Otis tarda*, a large lekking bird, stretches from Manchuria to the Iberian Peninsula across the grasslands and steppes of Eurasia (Isakov 1974, Collar 1996). The two subspecies of great bustard, European (*O. t. tarda*) and Asian (*O. t. dybowskii*) are geographically isolated and differ in coloration of neck, wing coverts and rectrices, patterning on the back, and extent of specialized display plumes on the chin and neck (Ivanov et al. 1951, Johnsgard 1991). While populations of the nominal subspecies are listed as Vulnerable (VU) worldwide by IUCN (BirdLife International 2012), only 1200–2200 Asian great bustards remain and this subspecies is Red-listed across its range of Russian South Siberia, Mongolia and China (Tseveenmyadag 2003, Goroshko 2008). Breeding grounds in Mongolia now represent the stronghold for this subspecies (Alonso and Palacín 2010). Clarification of threats to the subspecies and its natural history parameters, particularly in Mongolia, is identified as a priority for its conservation (Boldbaatar 1997, Chan and Goroshko 1998).

Detailed movement studies have not previously been undertaken on Asian great bustards, but data from radio and satellite tracking of the European subspecies indicate that great bustards display a wide range of migratory behaviors, including both partial and differential migration (Terrill and Able 1988). In general, migratory distance of great bustards increases longitudinally across Europe from west to east, in correspondence with severity of winter weather conditions and the degree of seasonality. A variety of short seasonal movements have been described in Spanish populations. These include post-breeding migrations by some males of up to 196 km, the distance of which may be dependent on climatic and habitat variables (Alonso et al. 2001, 2009). Some females make autumn/winter movements of up to 110 km (Alonso et al. 2000, Palacín et al. 2009); these migrations are culturally transmitted and condition-dependent (Palacín et al. 2011).

Great bustards in central Europe tend to be sedentary, though short migrations by some populations, or some individuals in a population, have been observed (Bankovics and Széll 2006). Irregular irruptive movements of up to 650 km have been recorded for these populations in response to severe winter weather (Faragó 1990, Block 1996, Streich et al. 2006).

Populations of European great bustards on the Lower Volga River in Russia – the most easterly populations for which tracking data are available – are mostly migratory. Females monitored via satellite telemetry traveled 1100 km over the course of approximately one week to winter in southeast Ukraine (Oparina et al. 2001, Watzke et al. 2001, Khrustov 2009).

Our group investigated the migratory behavior of Asian great bustards in north central Mongolia, approximately 4000 km east and 200 km south of the Volga populations. Given the severely continental climate of northern Mongolia, we predicted that distance migrated would be farther than observed in European populations, in correspondence with the longitudinal trends noted above. Here we present the first data on complete annual movements of this subspecies: the long-distance round-trip migrations of three female Asian great bustards.

Methods

Research was carried out on breeding populations of great bustards in east Khövsgöl Aimag, Mongolia (approximately 50°N, 101°E). Birds were found in valleys dominated by low-intensity agriculture (primarily summer wheat) and livestock herding by nomadic pastoralists. In this region of forest-steppe, winters are severe, with average January temperatures around −30°C (Inst. Geografii – Sibirskoe Otdelenie 1989). Nights and cold fronts in winter bring low temperatures of −40 to −50°C.

All work was carried out under permits issued by the Mongolian Ministry of Nature, Environment, and Tourism (no. 4/730, 4/1813, 6/1650) and using methods approved by the Arizona State Univ. Institutional Animal Care and Use Committee (no. 07-924R). We captured one female in 2007 and two additional females in 2008 by spotlighting (Giesen et al. 1982, Seddon et al. 1999, Geyser 2000).

Each bird was fitted with a solar-powered 70 g Argos/GPS platform transmitter terminal ('PTT') using a custom-fit backpack harness (modified from Osborne and Osborne 1998, Alonso et al. 2001). Stretchable silicone rope was threaded through bunched teflon ribbon to create a durable harness capable of adjusting to weight changes. The straps of the backpack cross at the breast, where they were stitched to ensure that the harness did not shift location. Points at which the harness was threaded through the transmitter were stabilized with instant glue. Birds were released at the site of capture within 15–30 min. The PTT and harness represent approximately 2% of the females' body weight, which falls within the range of loads recommended by Kenward (2001).

Each PTT transmitted GPS data (± 18 m accuracy) by radio signal to the Argos system (maintained by CLS, Toulouse, France) deployed on satellites. Duty cycles were tailored to maximize the number of GPS locations transmitted, with the length of day and strength of solar charge to the battery as limiting factors. Locations were recorded every two hours from 6:00 to 20:00 in spring and fall, from 4:00 to 22:00 in summer, and from 7:00 to 19:00 in winter. PTTs also reported speed of movement (± 1 km h^{-1} accuracy at speeds > 40 km h^{-1}). Upon receipt of a series of radio transmissions, the Argos system also estimates the location of the PTT using Doppler shift calculations, which are transferred in a separate data frame.

A comparison of the movements of individual tagged birds to each other, and to records of bustard migration at geographically similar locations, did not yield observations of consistent delays by any individual. We also did not observe correspondence between failure to breed and timing of spring arrival, which would indicate strong transmitter effects (Barron et al. 2010).

Routes were plotted and distances between points calculated using ArcGIS 10. Minimum convex polygons and kernel density estimations were created using Geospatial modelling environment (Beyer 2011). Departure and arrival dates were determined primarily through scrutiny of GPS-quality transmissions. We used Doppler-shift calculated locations when those allowed us to narrow the range of dates of a bird's arrival or departure in the absence of GPS-quality data.

Results

All three female birds were roughly the same weight at capture (Table 1). Birds no. 01 and no. 03 were captured in the same valley; bird no. 02 was captured in a valley 50 km distant. Data presented are of migratory movements from date of capture (Table 1) through 1 June 2009.

Table 1. Migratory activity recorded for three female great bustards *Otis tarda dybowskii* captured in north central Mongolia and harnessed with Argos/GPS satellite transmitters.

Bird ID	Capture date/weight	Season	Distance flown (km)	Start date	End date	Duration (days)	Mean km flown d^{-1}	Number of GPS points	Mean ground speed ± SD (km h^{-1})	n*
01	14 Jun 2007 3400 g	fall 2007	1954	13–16 Oct	4–12 Dec	49–60	33–40	56	59 ± 2	3
01	-	fall 2008	1852	17–19 Oct	4–6 Nov	16–20	93–116	19	59 ± 6	5
02	27 Jun 2008 3500 g	fall 2008	1836	12 Oct	31 Oct	19	97	56	87 ± 10	3
03	10 Jun 2008 3600 g	fall 2008	2044	17 Oct	18–20 Dec	62–64	32–33	205	76 ± 12	5
01		spring 2008	1966	24–26 Mar	28–31 May	63–68	29–31	39	62	1
01		spring 2009	1932	12–14 Mar	1 Jun	79–81	24	80	NA	–
02		spring 2009	1860	5 Apr	9–13 May	34–38	49–55	52	80 ± 6	2
03		spring 2009	2100	5 Apr	9 Jun	65	32	323	60 ± 9	8

*number of in-flight observations used to calculate mean flight velocity.

Due to radio interference typical in eastern Siberia and China and poor battery charge especially during winter months, not all logged GPS data were ultimately received by the Argos system. The greatest distance between any two successively received GPS points was approximately 1000 km, from Khövsgöl Aimag in Mongolia to the southern border of Mongolia, over a period of six days (bird no. 01, fall 2008).

Each female migrated from Khövsgöl Province in northern Mongolia in a southeastern direction (approximately 140°) to wintering spots near Xi'an city in Shaanxi Province, China (Fig. 1–3). Data indicate that the marked birds traveled independently of one another. Fall routes deviated from spring routes, but a consistent loop directionality was not detected. Average distance migrated was approximately 2000 km one-way, and was similar among birds and seasons (Table 1).

The migratory route of bird 01 in 2008 was similar to her route in 2007 (Fig. 1). In spring 2009 bustard 01 also performed a 50 km roundtrip detour in the direction of another known lek, where she spent 4–8 d before returning along the same path to resume her route northward.

The spring and fall migratory routes of bird 03 exhibited the most variation of the three birds tracked, with a maximum divergence of approximately 170 km (Fig. 2). This bird also took a detour of 60 km in northern Mongolia before returning to her primary lek in spring 2009.

Duration

Though distances traveled were similar among birds and seasons, we found five-fold variation among the three birds in the duration of migration. Average duration of a one-way trip was approximately two months (Table 1). In three of four cases, spring migration lasted longer than that bird's previous autumn migration. In the case of bird 01, spring 2009 migration was almost two months longer than the preceding fall migration (Table 1).

When in flight bird 02 regularly achieved speeds 30% greater than the other two birds, with a maximum ground speed of 98 km h^{-1}. The duration of her migrations was approximately half that of the other two birds (Table 1). Minimum ground speed recorded was 48 km h^{-1} for bird 03 in spring 2009.

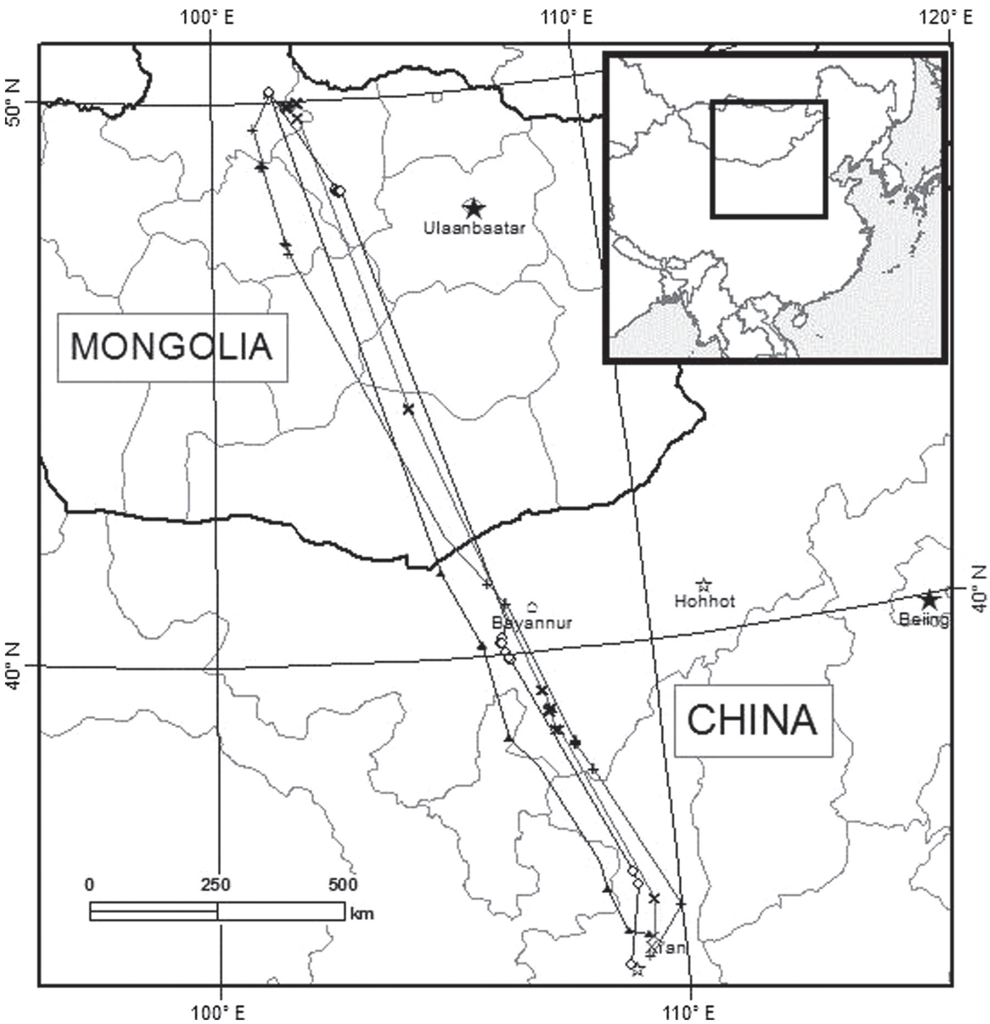

Figure 1. Map (UTM 47N projection) of the autumn 2007 (o), spring 2008 (+), autumn 2008 (▲) and spring 2009 (x) migratory routes of female great bustard *Otis tarda dybowskii* no. 01. Each vertex represents a GPS-quality stop location reported by the transmitter. GPS locations during flight were used to construct the path, but are not shown as vertices.

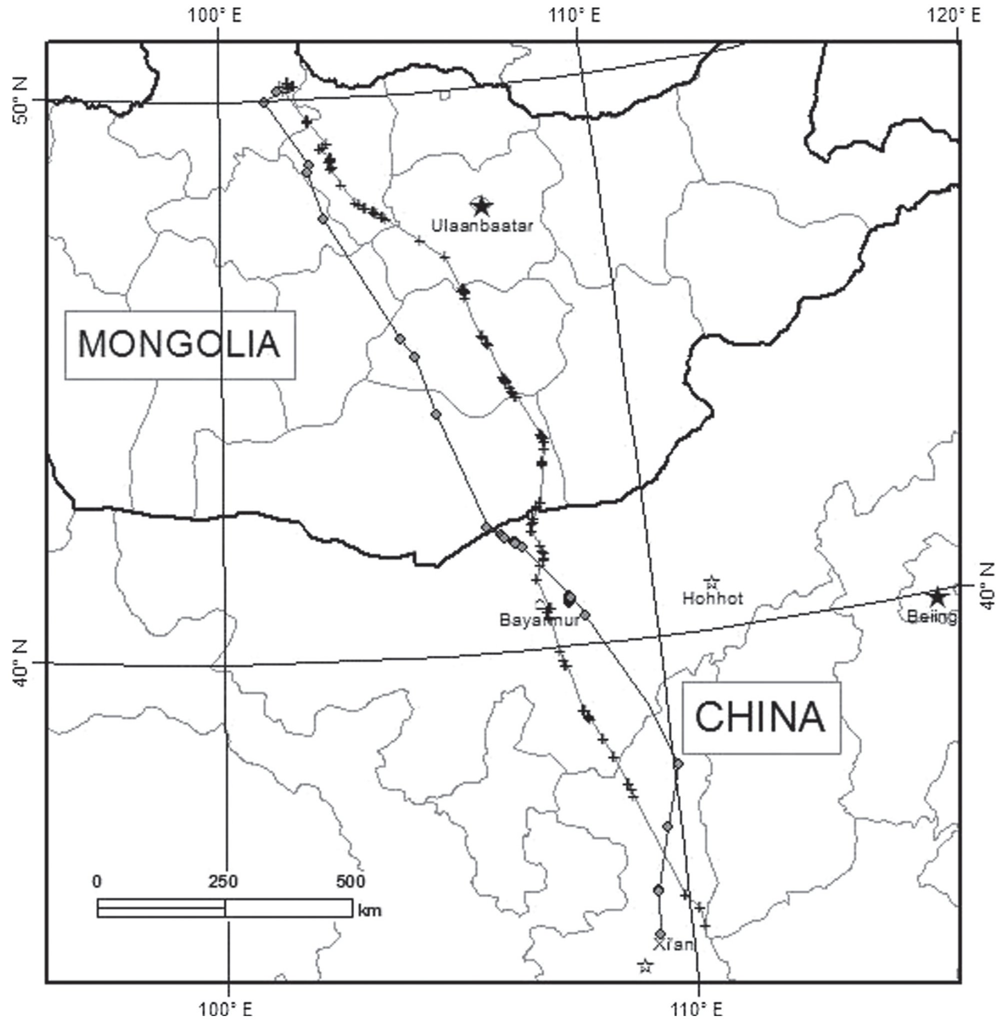

Figure 2. Map (UTM 47N projection) of the autumn 2008 (o) and spring 2009 (+) migratory routes of female great bustard *Otis tarda dybowskii* no. 03. Each vertex represents a GPS-quality stop location reported by the transmitter. GPS locations during flight were used to construct the path, but are not shown as vertices.

Stopover sites

The bustards we monitored used multiple and varied stopover sites, and it is likely that additional locations in which the birds stopped were not detected because of failed transmissions. We did not find fidelity to specific stopover localities. Most routes included a stop on the outskirts of Bayanur, an agricultural oasis in Nei Mongol, China, but stopovers there were spread across 130 km. Individuals occupied some stopovers for only 1–2 d and rarely took longer stops. Stops of approximately 10 d were recorded in Khishig-Öndör sum of Bulgan Aimag and Tarialan sum of Khövsgöl Aimag, Mongolia, and Ordos Prefecture and the Bayanur oasis in Nei Mongol, China. One stop of 45 d was recorded for bird 03 in the Bayanur oasis.

Wintering sites

These bustards overwintered in agricultural fields near the confluence of the Wei and Yellow Rivers in Shaanxi Province of China. Individuals tended to progress eastward through a series of non-repeated sites over the course of winter months, resulting in a large overall winter range (Fig. 4). The smallest range was recorded for bird 01 in winter 2008; this dataset also included the fewest observations and a gap in data reception of 107 d (Table 2). Bird 03 gradually moved eastward during the winter months, such that her first major northward movement was 90 km east of her last major southward movement (Table 2). Bird 02 also spent much of the winter moving gradually 50 km to the northeast.

Though birds 01 and 03 summer at the same lek in northern Mongolia, their wintering ranges did not overlap (Fig. 4). The ranges of birds 02 and 03 overlapped (Fig. 4), but the core areas used by each bird differed (Fig. 5). In 2008, bird 01 wintered 40 km north of the range she used in the previous winter.

Discussion

Migratory ecology

Geographic variation in migratory route

The migration routes we observed for Asian great bustards were twice as long as have previously been described for this species in the Lower Volga (Oparina et al. 2001) and 18 times

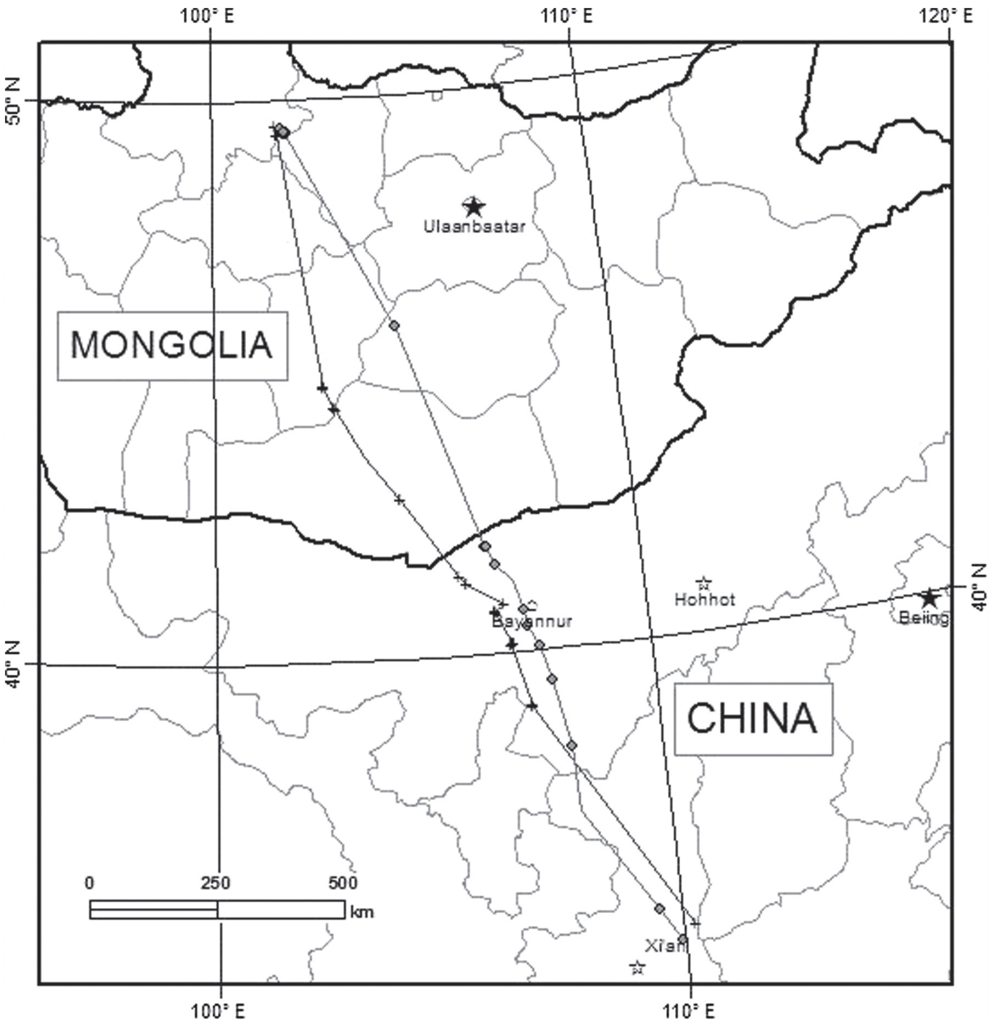

Figure 3. Map (UTM 47N projection) of the autumn 2008 (o) and spring 2009 (+) migratory routes of female great bustard *Otis tarda dybowskii* no. 02. Each vertex represents a GPS-quality stop location reported by the transmitter. GPS locations during flight were used to construct the path, but are not shown as vertices.

longer than those documented for female great bustards in Spain (Alonso et al. 2000, Palacín et al. 2009). Migratory distances thus increase longitudinally from west to east across the range of this species. Similar geographic variation has been reported in the migration of other Palearctic bustard species, which exhibit greater proclivity to migrate and undertake migrations of greater distance in the eastern portion of their ranges (Roselaar 1980, Combreau et al. 2011).

Murphy (1985) hypothesized that species exhibit biogeographical patterns reflecting increasing seasonality longitudinally from west to east across the western Palearctic. Meiri et al. (2005) found western Palearctic bird species (127 species in 14 orders) to show a greater tendency to migrate in eastern portions than in western portions of their ranges. Geographic variation has also been noted within bird species in the UK, where birds from areas with harsher climates made migrations of greater length than those from regions with milder climates (Siriwardena and Wernham 2002). Further, migration distance has decreased in European bird species as winter severity lessens with climate change (Visser et al. 2009).

Severity of winter weather increases longitudinally not only across Europe, but also into landlocked areas of central Eurasia (Borisov 1959). Mean low January temperatures are 30°C cooler and lowest recorded January temperatures are 36°C cooler in Khövsgöl than Madrid (Linés Escardó 1970, Lydolph 1977, World Meteorological Organization 1996). Seasonality increases longitudinally across this distance, with 18°C greater difference between mean July and mean January temperatures in Khövsgöl than in Madrid (World Meteorological Organization 1996). Thus, the longitudinal trend toward increased migratory behavior in great bustards is consistent with Murphy's hypothesis and the biogeographical findings of Meiri et al. (2005) and Siriwardena and Wernbaum (2002), and Asian great bustards represent the extreme of a longitudinal continuum of adaptation to severe climate. To put the degree of difference in climates into context, note that the mean annual range in temperature anywhere in Spain is similar to the mean daily range of temperature in our study region in northern Mongolia during the breeding season (20°C; Linés Escardó 1970, Lydolph 1977).

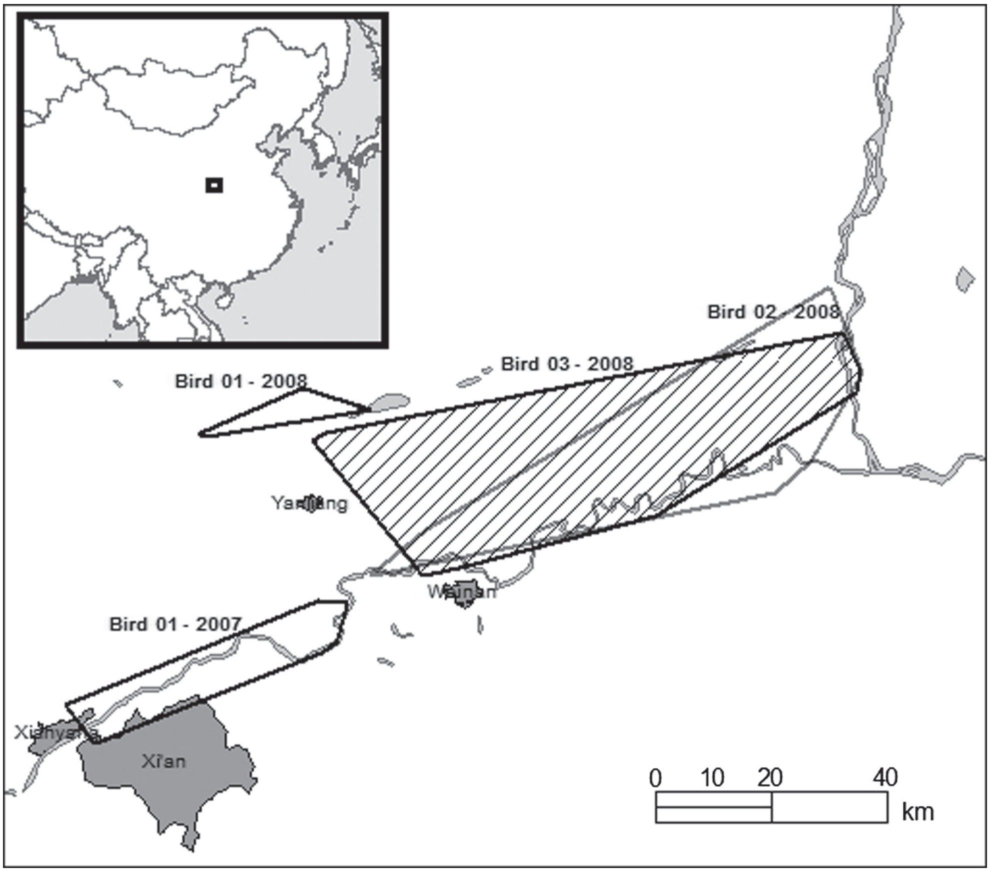

Figure 4. Map (UTM 47N projection) of the minimum convex polygons encompassing GPS locations at which each great bustard was recorded over the winter. Watercourses and urbanized areas are shaded.

Given these observations and the tendency of otherwise sedentary central European great bustards to migrate in adverse weather conditions (Streich et al. 2006), it is likely that harsh continental winters drive the observed long-distance migration of Asian great bustards breeding on the Mongolian Plateau. Indeed, northerly and northwesterly winds arising from the Siberian high-pressure system responsible for low winter temperatures in the region (Lydolph 1977, Gong and Ho 2002) may facilitate the southeasterly migration of great bustards. Variation in weather and forage conditions may cause variation in timing of migration of bustards from year to year (Kozlova 1975, Tseveenmyadag 2003).

In contrast to the severe winter temperatures described above for Khövsgöl Aimag, mean January temperatures in Xi'an, China, remain around 0°C (Watts 1969, World Meteorological Organization 1996). Through migration, great bustards may avoid not only cold temperatures, but also conditions of food shortage due to snow cover (Streich et al. 2006).

Stopover and wintering grounds and fidelity

We did not observe stopover site fidelity in the great bustards we monitored. This finding is in line with predictions for optimal migration in species that are not habitat specialists (Cantos and Tellería 1994), in that birds may reduce energy expenditure by correcting for wind drift only when approaching their final destination (Alerstam 1979, Catry et al. 2004).

Our study is the first to link a breeding population of Asian great bustards to their wintering grounds. Though we studied bustards breeding in north central Mongolia, additional breeding populations are scattered across central and eastern Mongolia (Tseveenmyadag 2003) and northeastern China (Gao et al. 2008). Given that these eastern breeding populations are subject to similar climatic and wind patterns, we hypothesize that the migratory routes of great bustards in eastern Mongolia parallel the southeasterly routes we have identified for central Mongolian bustards. If this hypothesis

Table 2. Wintering areas in China for three great bustards captured in northern Mongolia. MCP stands for minimum convex polygon.

Bird ID	Winter	Number of GPS points	Significant gaps in data (days)	Area of MCP (km^2)	Area of 80% kernel (km^2)	Maximum distance between points (km)	Ground speed	n*
01	2007–2008	49	12, 20, 18	401.7	63.7	51.7	61	1
01	2008–2009	26	107	86.1	35.8	29.6	NA	–
02	2008–2009	217	11, 16, 10	1450.7	355.7	93.8	64	1
03	2008–2009	200	17, 14, 12	1967.6	723.2	95.4	54	1

*no. of in-flight measurements received.

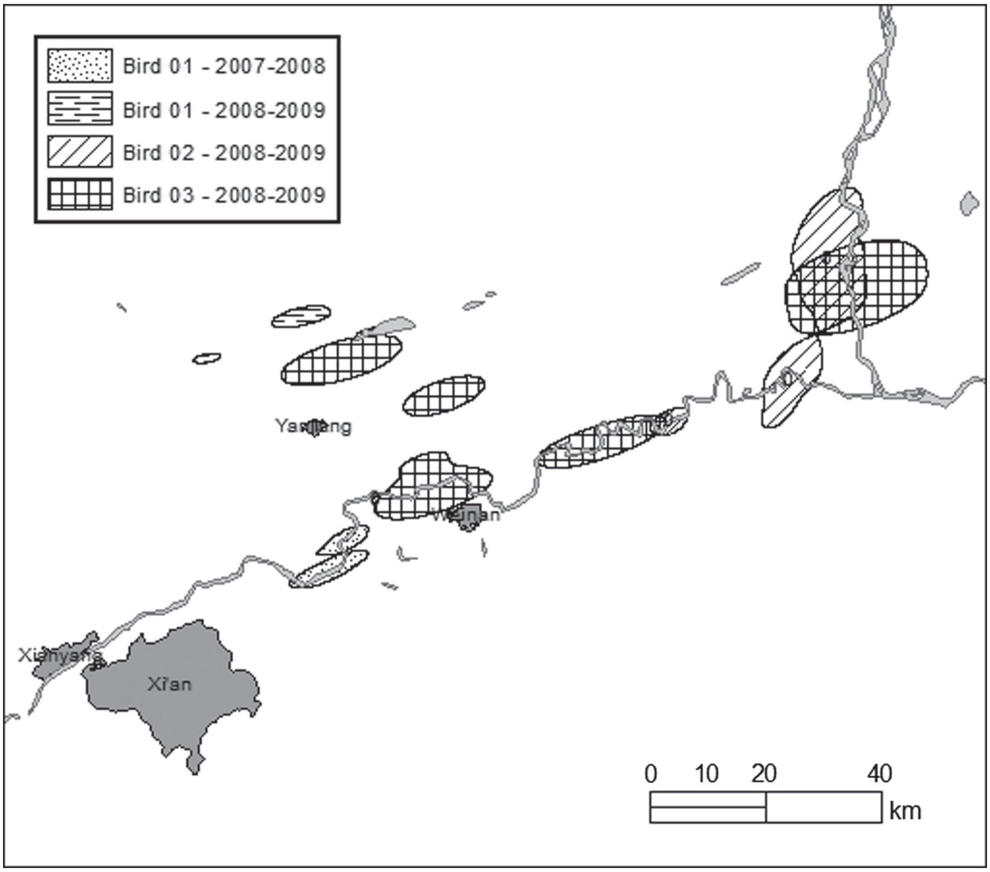

Figure 5. Map (UTM 47N projection) of 80% kernel density estimates of wintering areas used by each tagged great bustard. Watercourses and urbanized areas are shaded.

proves true, the overall effect of Asian great bustard migration would be a wide front gradually advancing through central and eastern Mongolia and China.

In contrast to behavior described in Spanish populations of great bustards, we observed winter site fidelity only at a regional scale. While winter home ranges of female bustards in Spain were less than 5 km in diameter (Alonso et al. 2000), the bustards we monitored occupied a series of locations across 30 to 95 km.

Migratory flight speed and duration

The bustards we monitored spent approximately one-third of the year on their migratory path. Active flight represented only 2–6% of the duration of each bird's migratory period. This extended migration period may be attributable to physiological and ecological constraints in heavier birds. Larger individuals are expected to stop more frequently and spend relatively more time at stopovers (Pennycuick 1989, Klaassen 1996, Hedenström and Alerstam 1998). A slow migration speed is typical of species which migrate later in autumn, and bustards are among the last migrants to depart northern Mongolia (Alerstam and Lindström 1990, Ellegren 1993, Yohannes et al. 2009). Finally, species which migrate diurnally, as do bustards, typically migrate more slowly than nocturnal migrants, most likely because they are limited to daylight hours for both flying and foraging (Hildén and Saurola 1982).

The range of migratory rates we observed for Asian great bustards overlapped with rates observed and expected for other large-bodied birds, such as swans, *Cygnus* spp., and geese, *Anser* spp. (Pennycuick 1989, Hedenström and Alerstam 1998). The houbara bustard *Chlamydotis undulata*, a sister species (Broders et al. 2003) which also breeds in central and inner Asia, exhibits migratory behavior similar to that we have observed in Asian great bustards (Combreau et al. 1999, Judas et al. 2006).

The shorter duration of fall migration, as compared to spring migration, undertaken by our tagged bustards contrasts with the general trend observed in European and African migrants (Newton 2008, Yohannes et al. 2009). However, a shorter fall migration may be typical in less well-studied inner Asia, where migrants face steeper environmental gradients in spring (Raess 2008). Further, Asian great bustards may be migrating with the aid of tail winds in fall, whereas in Europe the converse is the case (Kemp et al. 2010). It has also been suggested that long spring stopovers among another bustard species (houbara) may allow females to store reserves to be used for egg production immediately upon arrival at the breeding grounds (Tourenq et al. 2004).

Conservation across the migratory range

The female Asian great bustards we monitored spent two-thirds of the year at migratory stopover sites and wintering grounds. Given the large territory over which Asian great bustards range annually, the variety of threats they face, their use of human-dominated landscapes and nomadic behavior outside of the breeding season, it is clear that the conservation of Asian great bustards will require a broad-scale strategy and the integrated management of habitat between governmental agencies across provincial and international boundaries as well as the cooperation of local stakeholders (Boyd et al. 2008, Yorio 2009).

The use of multiple stopover sites and large wintering ranges increases the probability of encountering threats. Great bustards suffer mortality from collisions with overhead cabling and poisoning from agricultural chemicals and in Asia, poaching of great bustards is a major cause of adult mortality (Janss and Ferrer 2000, García-Montijano et al. 2002, Tseveenmyadag 2003). Additionally, climate change and land-use practices are increasing the extent of the Gobi Desert (Wang et al. 2008), a major migratory obstacle with limited forage for migrating bustards. Ongoing rapid development across the migratory range of these bustards will likely result in increased rates of mortality due to these causes, a challenge for a slow-maturing species with a low reproductive rate (Morales et al. 2002).

We suggest that the Asian subspecies of great bustard be included in Appendix of the Convention on Migratory Species, as has been done for middle-European populations of this species. A Memorandum of Understanding between China, Mongolia and Russia pertaining to the Asian great bustard could facilitate greater cooperation in the conservation of this threatened subspecies. Should Asian great bustard populations be lost, it may be difficult to later introduce individuals from western populations, which may lack adaptations to the Mongolian climate and to the long-distance migration we have described (Meiri and Yom-Tov 2004, Mettke-Hofmann and Greenberg 2005, Bowlin and Wikelski 2008, Hedenström 2008).

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