Asian Great Bustards: From Conservation Biology to Sustainable Grassland Development

by

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ABSTRACT

The Great Bustard (*Otis tarda*) is an iconic species of the temperate grasslands of Europe and Asia, a habitat that is among the least protected ecosystems in the world. A distinct subspecies, the Asian Great Bustard (*O. t. dybowskii*), is poorly understood due to its wary nature and remote range in Siberia, Mongolia, and northern China. This subspecies is now endangered by rapid development.

Using satellite telemetry and remote sensing, I investigated three aspects of the Asian Great Bustard's ecology critical to its conservation: migratory routes, migratory cues, and habitat use patterns. I found that Asian Great Bustards spent one-third of the year on a 2000 km migratory pathway, a distance twice as far as has previously been recorded for the species. Tracked individuals moved nomadically over large winter territories and did not repeat migratory stopovers, complicating conservation planning. Migratory timing was variable and migratory movements were significantly correlated with weather cues. Specifically, bustards migrated on days when wind support was favorable and temperature presaged warmer temperatures on the breeding grounds (spring) or advancing winter weather (fall). On the breeding grounds, Asian Great Bustards used both steppe and wheat agriculture habitat. All recorded reproductive attempts failed, regardless of habitat in which the nest was placed. Agricultural practices are likely to intensify in the coming decade, which would present further challenges to reproduction. The distinct migratory behavior and habitat use patterns of the Asian Great Bustard are likely adaptations to the climate and ecology of Inner Asia and underscore the importance of conserving these unique populations.

My research indicates that conservation of the Asian Great Bustard will require a landscape-level approach. This approach should incorporate measures at the breeding grounds to raise reproductive success, alongside actions on the migratory pathway to ensure appropriate habitat and reduce adult mortality. To secure international cooperation, I proposed that an increased level of protection should be directed toward the Great Bustard under the Convention on Migratory Species (CMS). That proposal, accepted by the Eleventh Conference of Parties to

CMS, provides recommendations for conservation action and illustrates the transdisciplinary approach I have taken in this research.

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CHAPTER 1

INTRODUCTION

A bird of superlatives, the Great Bustard (*Otis tarda*), is the heaviest bird capable of flight (Collar 1996, Bird 1999, Dunning Jr. 2008), displays the largest sexual size dimorphism of any bird species (Alonso et al. 2009a), and performs an elaborate breeding display (Johnsgard 1994). These characteristics make the Great Bustard an ideal flagship (Caro and O'Doherty 1999) for the conservation of the temperate grasslands that it inhabits. These grasslands are the world's least protected ecosystem (Scott et al. 2001, Brooks et al. 2004, Hoekstra et al. 2004), with the largest remaining expanses found in Central and Inner Asia (White et al. 2000). However, this habitat is threatened by rapid development as the region transitions from planned to free market economies (Reading et al. 2006, Batsaikhan et al. 2014).

The Great Bustard is also among the most threatened animal species in Inner Asia. The Asian subspecies ("Asian Great Bustard," *O. t. dybowskii*), found in eastern Russia, Mongolia and China, numbers only 2000 individuals (Tseveenmyadag 2001, 2003, Gombobaatar and Monks 2011). Naturally low reproductive rates make it difficult for this species to recover from declines (Morales et al. 2002, Zhao et al. 2006). While studies of European populations of Great Bustards are extensive (Raab 2015) and their conservation highly managed, Asian Great Bustards have received scant attention.

Chapters Two through Four of my dissertation each explore a facet of the Asian Great Bustard's ecology critical to its conservation: Chapter 2) migratory routes; Chapter 3) migratory cues; and Chapter 4) habitat use patterns. The range of the Great Bustard stretches 10,000 km from Portugal to northeastern China, which provides a unique opportunity to understand the adaptations of this species to vastly differing climatic and habitat conditions. Throughout my dissertation, I compare and contrast my results with studies of the European Great Bustard subspecies (*O. t. tarda*) to reveal behavioral and ecological adaptations of the Asian Great Bustard. Chapter Five presents a summary of previous research on Great Bustards and the threats the species encounters across its range. This chapter takes the form of a proposal to increase international protection for the species, and its second role in my dissertation is to illustrate the transdisciplinary approach I have employed in my work, outlined below in “Impact.”

APPROACH

Due to the exceptional wariness of Great Bustards in Asia, the remote and difficult terrain they inhabit, and economic limitations, previous research on Mongolian Great Bustards has consisted only of intermittent, localized population surveys (Goroshko and Natsagdorjin 2000, Tseveenmyadag 2001, Batsaikhan 2002). The first year of my field research was devoted to identifying remnant populations of Great Bustard suitable for a long-term research project (i.e., populations with greater than 10 breeding individuals). The low number of remaining Great Bustards in this region restricts research methods, both logistically, in terms of the time required e.g., to locate individuals for research each day, and ethically, in that research methods must minimize risk of harm to the birds. The most suitable populations for study are located in remote areas of the countryside that present additional logistical restraints on research, including lack of power, communication, and transportation infrastructure. Further, my research was embedded within a rural, conservative Mongolian community which necessitated observation of traditional mores, e.g., a ban on handling eggs.

Under these conditions, I chose to employ satellite telemetry as a primary research tool. Satellite telemetry requires a single capture event, after which these wary birds can be monitored without the confounding factor of human presence. Satellite telemetry also enables collection of data throughout the annual cycle and across the migratory cycle of these birds. I found geographic information systems, remote sensing, and spatial statistics to be vital tools in the analysis of movement patterns and habitat use of this long-ranging bird.

CHAPTERS

Chapter Two: Migration routes

An understanding of migratory routes is important for the conservation of a species (Moore et al. 1995, Bibby 2003, Newton 2004). In Chapter Two, I present the first report of the migratory behavior of Asian Great Bustards, obtained through satellite telemetry. A comparison of my findings to those of other researchers across this species' range also permits analysis of longitudinal variation in migratory behavior and the range of adaptations this species displays to Eurasia's diverse climates. While European Great Bustards are sedentary or make a series of short seasonal movements in the Mediterranean climate of Spain and Portugal (Alonso et al. 2000), I found Asian Great Bustards breeding in the highly continental climate of northern Mongolia to undertake regular, long-distance migrations. The birds I monitored spent one-third of the year on multiple and non-repeated stopovers, and moved nomadically across large winter ranges. These movement patterns complicate efforts to preserve habitat and reduce causes of adult mortality. These observations prompted me to pursue the development of policy mechanisms for international cooperation presented in Appendix A.

Chapter Three: Migration cues

Effective conservation policy considers not only current conditions but also anticipates foreseeable changes to a species' habitat. In Chapter Three, I explore the connection between weather and migratory behavior of Asian Great Bustards to inform predictions about future migratory behavior of these populations under climate change conditions. I also use this research as a case study in a larger debate concerning the nature of control of migratory behavior in birds. I found Asian Great Bustards to exhibit plasticity in their migration phenology, including a wide range of inter- and intra-individual variation in departure dates. I found correspondence between migratory movements and weather conditions, particularly wind and temperature. My findings fit into a broader picture of the Great Bustard as a species responsive to weather cues: though inhabiting much milder climates, European Great Bustards move in response to both summer heat (Alonso et al. 2009b) and severe winter weather events (Faragó 1990). A flexible migration strategy may allow Great Bustards to adjust more rapidly to changing climatic conditions.

Chapter Four: Habitat use patterns

Provision of conditions appropriate for successful breeding are particularly important for this species, which exhibits a naturally low reproductive rate that is often further dampened by human activity (Ena et al. 1987, Rocha et al. 2013). Even small changes in the reproductive rate of populations of Great Bustards result in large changes in extinction probability (Lane and Alonso 2001). In Chapter Four, I examine the habitat use patterns of Great Bustards during the breeding season as well as reproductive success in relation to nest site selection. In contrast to Europe, the development of large-scale agriculture within the Asian Great Bustard's range is relatively recent and ongoing. Therefore, the populations I studied provide a window into the process of Great Bustard adaptation to human modification of the steppe habitat. While some European Great Bustards now actively avoid unmodified steppe (Lane et al. 2001, Moreira et al. 2004, Watzke 2007), I found that Asian Great Bustards used steppe and agricultural habitat at similar rates, though the availability of steppe was higher. I posit that a distinctive feature of the Asian subspecies is its tolerance of forest edge habitat, particularly for nesting. All reproductive efforts I recorded failed, regardless of the habitat in which they were located, raising conservation concern.

Appendix A: Proposal to increase international protection for the Great Bustard

The fifth chapter of my dissertation takes the form of a proposal to the Convention on the Conservation of Migratory Species of Wild Animals (CMS) (Caddell 2005) to increase international protection for Great Bustards. In this chapter, I provide background on the status of this species and the threats it faces across its range. I also translate what I have learned from field studies into actionable policy recommendations. This document was advanced by the Government of Mongolia and accepted by the plenary of the Eleventh Meeting of the Conference of Parties to CMS. This established a framework for international coordination in the conservation of the Asian Great Bustard.

IMPACT

Although it is essential to understand the behavior and ecology of a species to plan for its conservation, the implementation of those plans ultimately requires a change in the attitudes and actions of people. A transdisciplinary approach to conservation research works toward this goal by engaging stakeholders at multiple levels (Tress et al. 2005, Reyers et al. 2010) and in doing so, results in greater effect on public policy (Evely et al. 2010).

Just as my research reaches across multiple spatial scales, from the nesting site to the annual migratory route, I sought to engage people from the herders at the bustards' breeding grounds to international organizations. At my field site in northern Mongolia, I involved local people in research activities, provided opportunities for employment and training to rural communities, carried out environmental education programs for nomadic schoolchildren and the Buddhist monastic community, and built scientific capacity by supporting the education of local undergraduate and master's students. At the national level, I collaborated with non-governmental organizations, communicated findings and recommendations to the government, and shared information with the urban population through production of a television documentary. I contributed to conservation policy documents for international development organizations and developed dialogue and mutual support amongst researchers working on bustard species across Eurasia. For the purpose of developing international cooperation vital for migratory populations of Great Bustards, I spearheaded an effort to advance the level of protection afforded this species under the auspices of the Convention on Migratory Species (Chapter Five).

My hope is that the work I have done through my dissertation research not only expands our understanding of the biology of the Great Bustard, but contributes in an immediate way to the survival of Asian populations and their habitat. I also hope that this project has contributed to the vitality of the rural communities that have taught me much about the Great Bustard, and who ensure the persistence of this species in the wild.

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CHAPTER 2

SATELLITE TELEMETRY REVEALS LONG-DISTANCE MIGRATION IN THE ASIAN GREAT BUSTARD *Otis tarda dybowskii*

ABSTRACT

The range of the Great Bustard stretches 10,000 kilometers 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, 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.

INTRODUCTION

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 the Asian 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 (cf. Terrill & 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 (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 (Institut 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 Mongolian Ministry of Nature, Environment, and Tourism (#4/730, 4/1813, 6/1650) and using methods approved by the Arizona State University Institutional Animal Care and Use Committee (#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 70g Argos/GPS platform transmitter terminal ("PTT"; Microwave Telemetry Inc., Columbia, USA) using a custom-fit backpack harness (modified from Osborne and Osborne 1998; Alonso *et al.* 2001). Stretchable silicone rope (PolyMax, Hampshire, UK) was threaded through bunched Teflon ribbon (Bally Ribbon Mills, Bally, USA) 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 minutes. 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/hr accuracy at speeds >40 km/hr). 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 (ESRI, Redlands, USA). 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 #01 and #03 were captured in the same valley; bird #02 was captured in a valley 50 km distant. Data presented is of migratory movements from date of capture (Table 1) through 1 Jun 2009.

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 #01, fall 2008).

Each female migrated from Khövsgöl Province in northern Mongolia in a southeastern direction (approximately 140º) to wintering spots near Xi'an city in Shaanxi Province, China (Figures 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 days 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/hr. The duration of her migrations was approximately half that of the other two birds (Table 1). Minimum ground speed recorded was 48 km/hr for bird #03 in spring 2009.

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 days and rarely took longer stops. Stops of approximately 10 days 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 days 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 days (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 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). At the extremes, 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).

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 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, a major migratory obstacle with limited forage for migrating bustards (Wang et al. 2008). 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 I 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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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/Day	Number of GPS points	Mean Ground Speed ± S.D. (km/h)	n*
#01	14 Jun 2007 3400g	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 3500g	Fall 2008	1836	12 Oct	31 Oct	19	97	56	87 ± 10	3
#03	10 Jun 2008 3600g	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

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

* Number of in-flight measurements received

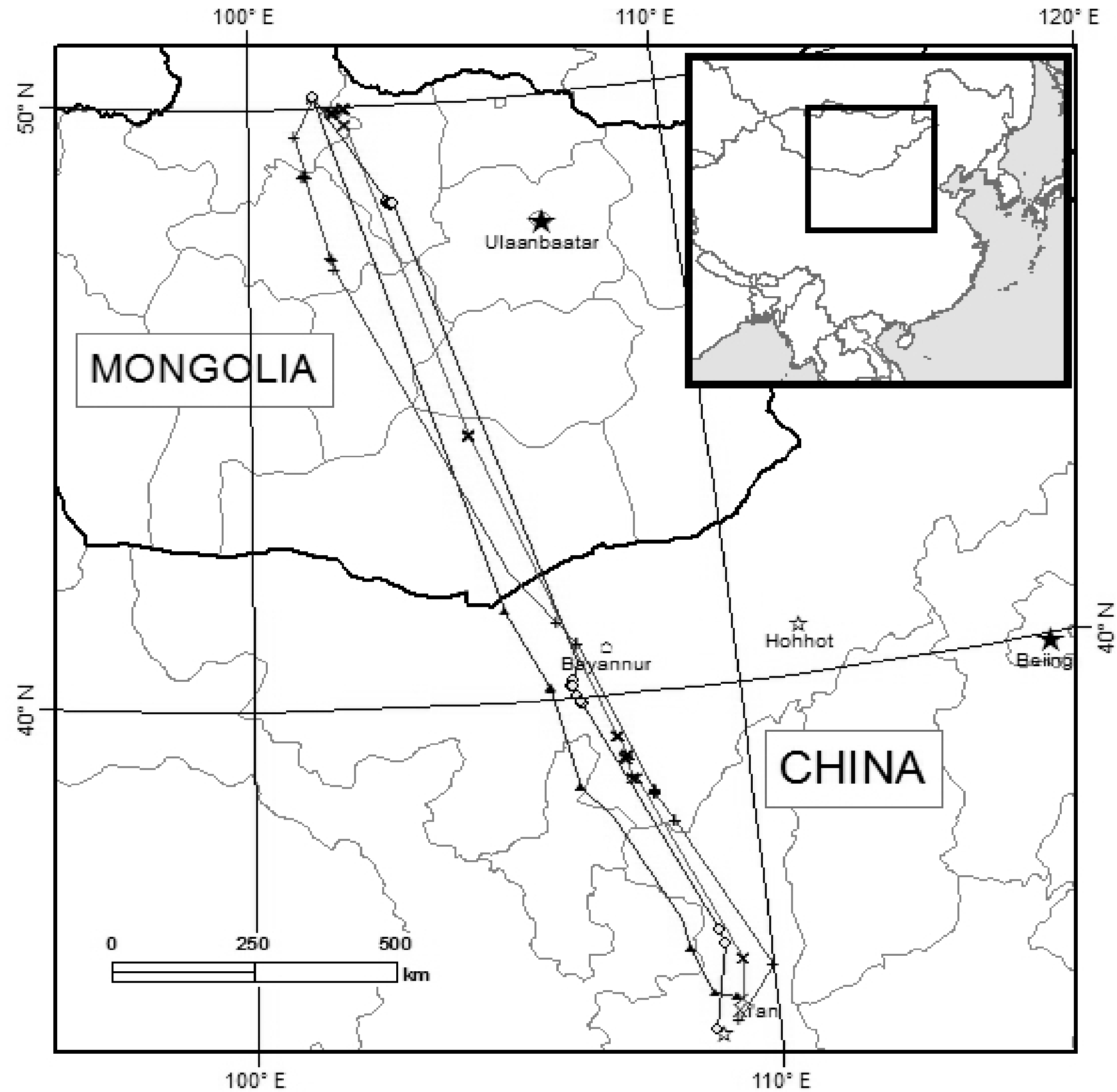

Figure 1. Map (UTM 47N projection) of the autumn 2007 (o), spring 2008 (+), autumn 2008 (▲) and spring 2009 (x) migratory routes of female Great Bustard (*Otis tarda dybowskii*) #01. Each vertex represents a GPS-quality stop location reported by the transmitter. GPS locations during flight were used to construct the path, but are not shown as vertices.

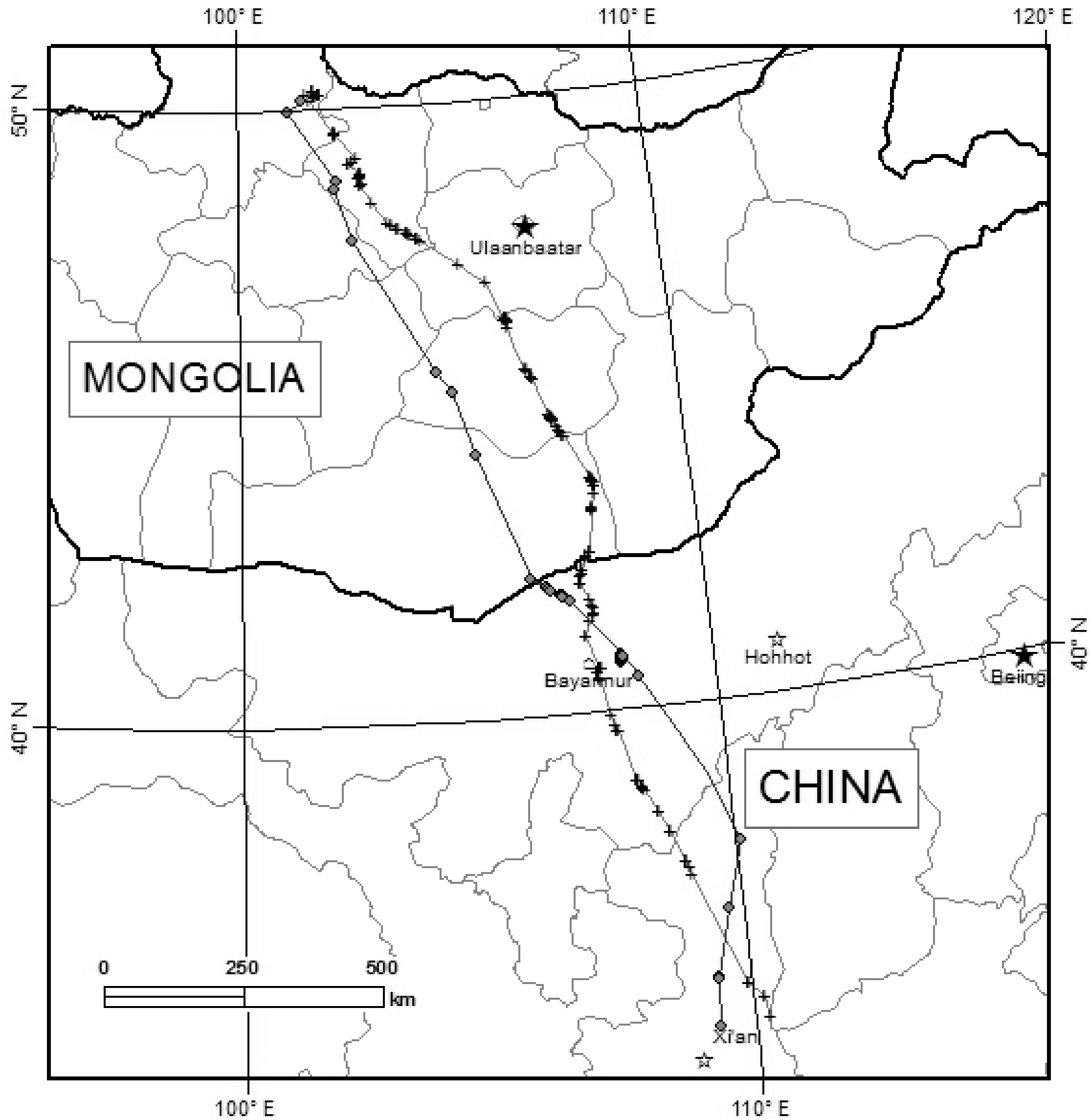

Figure 2. Map (UTM 47N projection) of the autumn 2008 (o) and spring 2009 (+) migratory routes of female Great Bustard (*Otis tarda dybowskii*) #03. Each vertex represents a GPS-quality stop location reported by the transmitter. GPS locations during flight were used to construct the path, but are not shown as vertices.

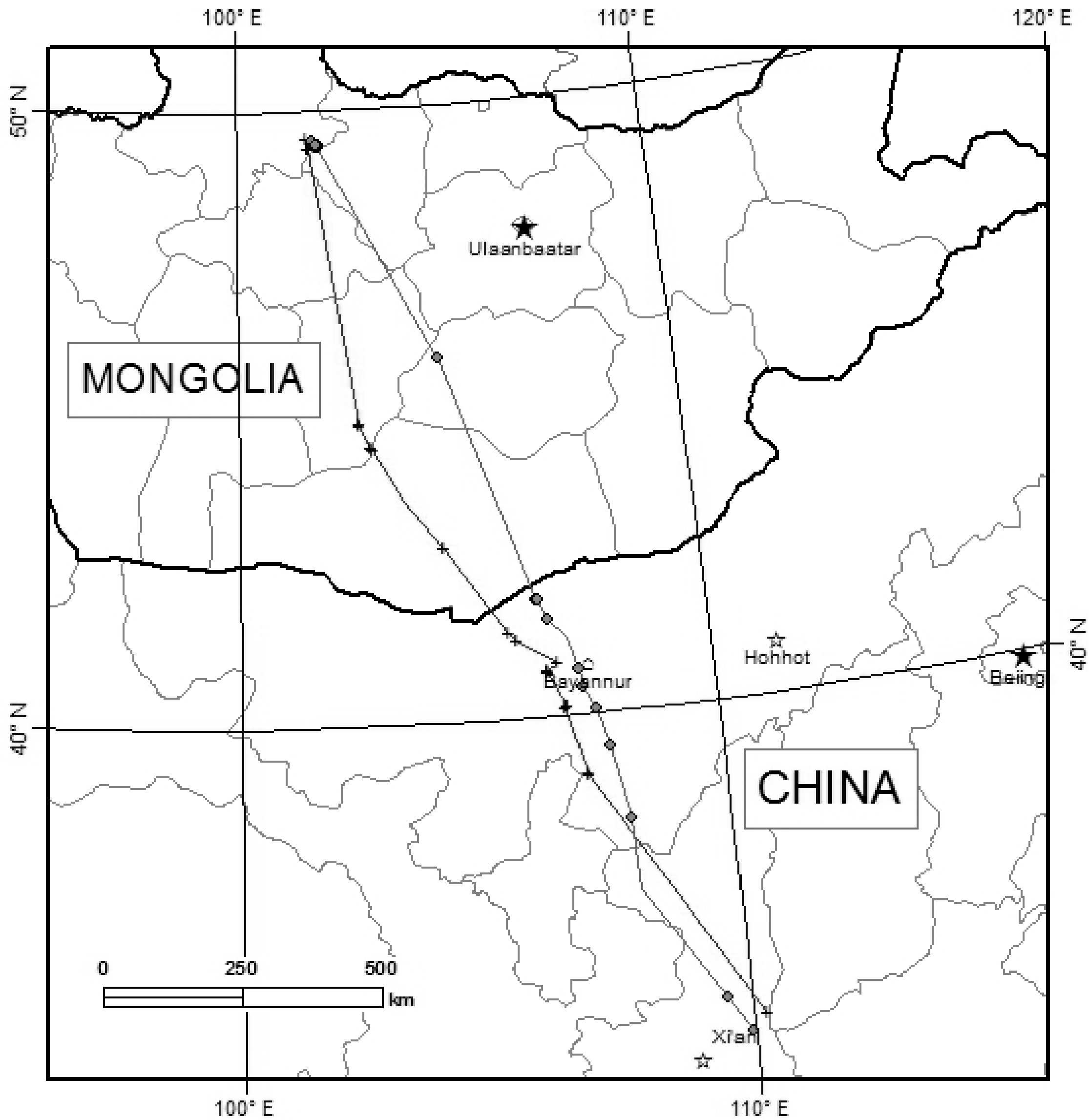

Figure 3. Map (UTM 47N projection) of the autumn 2008 (o) and spring 2009 (+) migratory routes of female Great Bustard (*Otis tarda dybowskii*) #02. Each vertex represents a GPS-quality stop location reported by the transmitter. GPS locations during flight were used to construct the path, but are not shown as vertices.

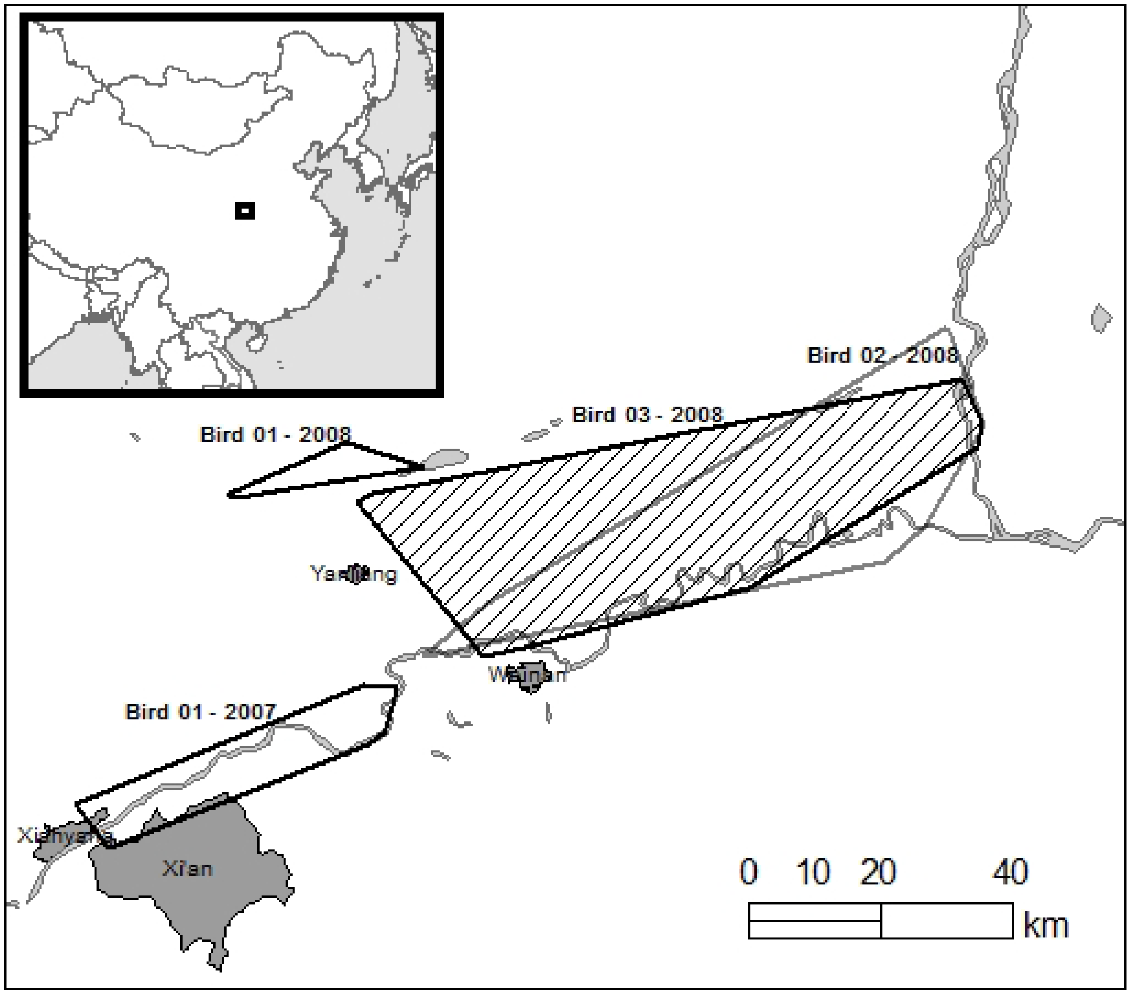

Figure 4. Map (UTM 47N projection) of the minimum convex polygons encompassing GPS locations at which each Great Bustard was recorded over the winter. Watercourses and urbanized areas are shaded.

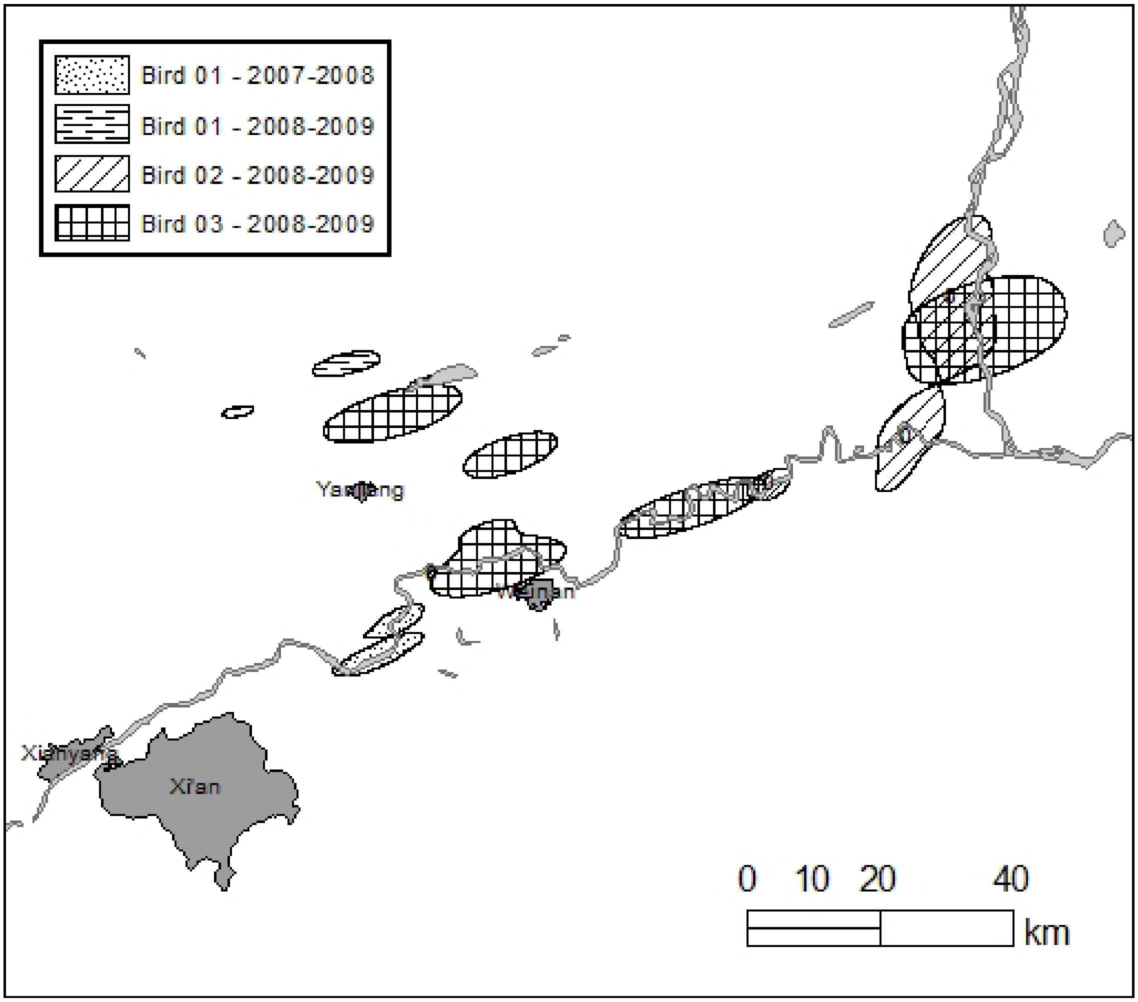

Figure 5. Map (UTM 47N projection) of 80% kernel density estimates of wintering areas used by each tagged Great Bustard. Watercourses and urbanized areas are shaded.

CHAPTER 3

EVIDENCE FOR FLEXIBLE MIGRATORY BEHAVIOR IN FEMALE ASIAN GREAT BUSTARDS (OTIS TARDA DYBOWSKII)

ABSTRACT

Breeding ground arrival dates for many migratory bird populations have advanced in recent decades. Two hypotheses have been proposed to explain shifts in individual migratory strategy: 1) natural selection has favored individuals whose migratory activity (*zugunruhe*) is triggered by shorter photoperiod or 2) migratory timing is plastic and responds to climatic cues. I examined these two hypotheses by longitudinally monitoring migration in female Asian Great Bustards (*Otis tarda dybowskii*) using satellite telemetry. Timing of migratory arrivals and departures for individuals monitored more than one year was highly variable, with interannual differences ranging from 7 to 79 days. Inter-individual variation in migratory timing ranged from 42 days (spread of spring arrival at the breeding grounds) to 99 days (fall departure from breeding grounds). I also found correspondence between migratory movements and weather conditions, particularly temperature and wind. Taken together, these findings suggest that the migration phenology of Asian Great Bustards is flexible and influenced by environmental conditions. Breeding ground arrival advanced with each additional year of monitoring, which indicates a degree of plasticity attributable to learned experience. Early arrivals are facilitated by early departure from the wintering grounds rather than by increased speed of migration. Though two individuals made the 2000 km migratory journey in as little as one to eight days, the average one-way journey took 50 days. In contrast to what has been found for many migratory birds, spring migration of Asian Great Bustards was not shorter in duration than fall migration. These long-distance migrants may time arrival at the breeding grounds by reassessing conditions at each migratory stopover. Such plasticity could allow for more rapid adjustment to a variable and changing climate. However, climate predictions across the annual range suggest future conditions that may both positively and negatively impact population levels of this endangered subspecies.

INTRODUCTION

A range of changes in migratory behavior of birds have been attributed as adaptations to climate change. While some populations have shortened their migratory distance by overwintering at locations closer to the breeding grounds or shifted to partial migration (Sutherland 1998, Siriwardena and Wernham 2002, Visser et al. 2009, Heath et al. 2012), others now breed at higher latitudes or elevations (Thomas and Lennon 1999, Böhning-Gaese and Lemoine 2004, Devictor et al. 2008). The most widely reported change is the advancement of arrival of bird populations to breeding grounds, though these advancements are often not uniform and timing within a single species may vary by geographic region or year (Bradley et al. 1999, Cotton 2003, Lehikoinen et al. 2004, Rubolini et al. 2007, Gordo 2007, Lehikoinen and Sparks 2010, Courter et al. 2013). Multispecies studies find no overarching taxonomic tendency in likelihood and type of migratory change, however, late migrating species appear to have further delayed their fall migration while early migrators advanced their departure (Siriwardena and Wernham 2002, Miholcsa et al. 2009).

The proper timing of arrival at breeding grounds is important because early arrival can offer significant benefits, but may come with significant risks. Early arriving individuals may now arrive when resource availability is peaking, if advancing phenology of insect and plant resources allow for greater production, provisioning, and survival of offspring (Visser and Both 2005, Parmesan 2006, Both et al. 2010). In contrast, there may be strong selection against early arrival, if poor weather and lack of resources increase the risk of mortality or reproductive failure (Brown and Brown 2000, Both et al. 2010). While many migratory bird species are experiencing population declines (Sanderson et al. 2006), migratory species that have advanced their arrival dates tend to have a better conservation status than those that have not (Møller et al. 2008), making it important to understand the mechanisms by which these behavioral shifts develop.

Hypotheses explaining shifts in migratory phenology

Two hypotheses have been proposed to explain the mechanism underlying advancement in migratory arrival date (Gienapp et al. 2007), which are not mutually exclusive. The “microevolutionary” hypothesis presupposes rigid, genetic control of migration, entrained over evolutionary time by predictable seasonal change in photoperiod (Farner 1950, Gwinner 1996, Both and Visser 2001). Individuals may show heritable variation in photoperiodic response and thus migratory timing, but with a recent shift in climate, natural selection has favored individuals with a genetic predisposition to migrate earlier in spring (Jonzén et al. 2006, Sheldon 2010). Laboratory experiments indicate that timing of migratory activity (*zugunruhe*), as well as physiological preparation in the form of fat deposition and moult, are correlated with photoperiod (Gwinner et al. 1985, Gwinner 1996) and are genetically heritable (Berthold 1988), providing support for the role of endogenous control in timing of migratory behavior. However, data supporting a genetic role in observed shifts in timing are few, and there is doubt that evolutionary processes could occur rapidly enough to explain these changes (Gienapp et al. 2007, 2008, Hendry et al. 2008). The microevolutionary hypothesis has been advanced particularly for longer-distance migrants, which presumably have fewer indicators of conditions on the breeding grounds (Both and Visser 2001, Butler 2003), though evidence for this claim is mixed (Knudsen et al. 2011).

The “individual plasticity” hypothesis emphasizes the ability of an individual to vary its arrival date from year to year in response to environmental conditions (Gienapp et al. 2007, Knudsen et al. 2011). Under this scenario, endogenous control of migratory movement is tempered by individual plasticity, which hastens or delays migration until weather conditions are appropriate. While shorter-distance migrants may be able to more easily assess weather conditions at their breeding grounds (Hötker 2002), longer-distance migrants may rely on large-scale correlation in weather patterns (Saino and Ambrosini 2007), detection of infrasound signs of severe weather conditions (Streby et al. 2015) or make use of a step-by-step approach to migration, reassessing conditions at each migratory stopover (Tøttrup et al. 2010). Evidence supporting a significant role for phenotypic plasticity include observations correlating earlier population-level arrivals to changes in climate, as described above. Conditions on the wintering grounds and migratory stopovers have also been correlated with migratory timing, with those occupying higher-quality wintering territories and stopovers arriving on breeding grounds earlier

(McNamara et al. 1998, Saino et al. 2004, Gunnarsson et al. 2006, Hüppop and Winkel 2006, McNamara and Houston 2008, Balbontín et al. 2009).

Examining migratory movement across the annual range

In this study, I combined longitudinal satellite tracking with newly available global weather datasets to examine the role of endogenous control and plasticity in determining the migratory timing of female Asian Great Bustards (*Otis tarda dybowskii*). Before the advent of satellite tracking, most studies of migration strategy relied on visual or radar observations at the population level including records of first arrivals, rates of passage, or limited data on individuals from banding records (e.g. Richardson 1978, Biebach et al. 2008). Improvements in tracking technology have made possible longitudinal monitoring of individuals at high spatial and temporal resolution. Multi-year satellite tracking datasets have been identified as a priority for animal movement studies as they are better suited to evaluate the degree of individual plasticity in timing of migration and allow insight into development and change in movement patterns over the lifetime of an individual (Holyoak et al. 2008, Knudsen et al. 2011, Wikelski 2014).

Analyses of the impacts of weather on migratory movement have historically been constrained by observer viewpoint, with most research describing weather conditions upon migrant arrival in spring and departure in fall (Newton 2008, Knudsen et al. 2011). Advances in remote sensing, large-scale data collection and computer processing now provide the opportunity to examine fine-scale relationships between individual movements and environmental conditions across the migratory pathway, which has also been identified as a priority for animal movement research (Holyoak et al. 2008).

However, as of yet, studies combining fine-scale environmental data and satellite tracking to examine migratory timing are rare. Klaassen et al. (2004), Hawkes et al. (2011), and Mandel et al. (2008) examined the relationship of migratory movements of Bewick's Swans (*Cygnus columbianus bewickii*), Bar-Headed Geese (*Anser indicus*), and Turkey Vultures (*Cathartes aura*), respectively, to wind conditions. Dodge et al. (2014) investigated Turkey Vulture migratory movements in relation to temperature and thermal columns in the only multi-year study of this type of which I am aware. The primary emphasis of these investigations has been physiological questions concerning metabolic demands of flight.

Migratory movement in Great Bustards

Satellite monitoring has elucidated the migratory patterns of European Great Bustards (*Otis tarda tarda;* Alonso et al. 2000a, b), Asian Houbara Bustards (*Chlamydotis macqueenii*; Launay et al. 1999, Combreau et al. 2011), Little Bustards (*Tetrax tetrax;* Villers et al. 2010), and Australian Bustards (*Ardeotis australis*; Ziembicki 2009). The seasonal movements of European Great Bustards and Australian Bustards have been correlated with regional climate characterizations (Alonso et al. 2009, Ziembicki 2009). However, my research is the first to connect migratory movements with daily weather patterns in any bustard species (Otididae). Great Bustards are diurnal migrants and migrate by flapping flight. The Great Bustard performs a variety of migratory behaviors across its 10,000 km range, with more easterly populations exhibiting increasing propensity to migrate and migrations of longer duration. Iberian populations make a variety of short seasonal movements (Alonso et al. 2000b, Palacín et al. 2009), while central European Great Bustards are primarily sedentary, migrating only in response to exceptional weather conditions (Hummel 1985, Faragó 1990, Streich et al. 2006). To the east, populations breeding in European Russia perform regular migrations of 1000 km over the course of one week (Oparina et al. 2001, Watzke 2007). Female Asian Great Bustards regularly migrate 2000 km from northern Mongolia to central China over the course of approximately two months (Kessler et al. 2013). Where Great Bustards are regular migrants, they are among the last species to migrate in autumn and among the earliest to arrive in spring. At the population level, a large degree of inter-annual difference in the migration timing of Great Bustards has historically been noted (Kozlova 1975, Yakushev et al. 2004).

Understanding the migratory response of the Great Bustard to climate change is particularly important for conservation of the eastern populations of this species. Though the species is listed as Vulnerable worldwide (BirdLife International 2014), populations in Asia are at greater risk. Only 300 to 1000 individuals of the nominate subspecies remain in Central Asia

(Mityaev and Yashchenko 2006, Gubin 2007), while 2000 individuals of the eastern subspecies remain in Siberian Russia, Mongolia, and China (Tseveenmyadag 2003). The regular migration performed by these populations poses a number of challenges to their conservation, including poaching and collision with power lines at multiple and irregular stopovers (Tseveenmyadag 2003, Kessler et al. 2013). Additionally, the timing of Great Bustard arrival and reproduction in the agricultural mosaics these birds use as breeding grounds must be understood to develop plans for timing of the use of agricultural machinery in a manner that enables crop production without destroying Great Bustard clutches.

Hypotheses and predictions

To elucidate methods for control of migratory behavior in Asian Great Bustards, I first examined arrival and departure dates of longitudinally monitored individuals. Should there be strong endogenous control of migration, I expected to observe relatively consistent interannual migratory timing within individuals, presupposing interannual consistency in conditions at the wintering grounds. Second, I investigated whether the migratory movements of individual bustards are correlated with weather conditions.

During winter, the female Asian Great Bustards I monitored moved nomadically through the Guanzhong Plain, where winter temperatures average 0˚C in January (Watts 1969, World Meteorological Organization 1996). In this region, approximately 200-300 Asian Great Bustards overwinter in 500,000 ha of irrigated fields, where they feed on crop stubble and dry grasses (Wang 2010). Tagged bustards migrated independently and used stopovers varying by up to 450 km from east to west, such that they encountered differing weather conditions in passage. Should control of migration in bustards be tempered by a plastic response to environmental cues, I expected to detect both inconsistent interannual migratory timing within individuals and correlation between environmental conditions and migratory movements.

To identify potential migration cues, I examined a variety of weather variables that have previously been connected to avian migratory movement and which may be relevant to the ecology of the Great Bustard, including wind, atmospheric pressure, precipitation, and temperature. Research has indicated that wind direction and speed are key considerations for timing of migratory movements (Alerstam 1990, Åkesson and Hedenström 2000, Green et al. 2002, Liechti 2006), as the degree of wind support makes a significant difference in energetic cost and duration of migration. I expected that female Asian Great Bustards, like similarly sized Bewick's Swans (Klaassen et al. 2004) would be more likely to undertake migratory movements on days with stronger wind support and less crosswind.

Changes in barometric pressure frequently accompany precipitation events, changes in temperature, wind direction and speed as a new weather system moves into a geographic region. A migratory movement in relation to changing barometric pressure may represent avoidance of impending weather conditions, or the usage of advantageous winds associated with the weather front. Allen et al. (1996) attribute the tendency of falcons to migrate on the day of frontal passage to the increased ground-level wind speeds and favorable wind direction associated with the front, and falcons' reliance on powered flight. A regional atmospheric pressure phenomenon that may influence migration is the Siberian Anticyclone, a recurrent, large-scale, high-pressure cell in north Asia. The Siberian Anticyclone arises in autumn and brings clear skies, cold temperatures, and southeasterly winds opportune for Great Bustard migration (Lydolph 1977, Gong and Ho 2002). Conversely, reduction of the Siberian Anticyclone could ease northbound Great Bustard migration in late spring. The Arctic Oscillation Index (AOI), which characterizes weather patterns in the northern hemisphere (Thompson and Wallace 1998), is negatively correlated with the Siberian Anticyclone (Gong et al. 2001). I thus expected Great Bustard migratory movements to correspond with low values for the AOI in fall, when southeasterly winds would aid migration, and high values in spring, when anticyclone winds would represent a headwind (see Zalakevicius et al. (2006) for analogous use of the North Atlantic Oscillation Index).

Precipitation has also been connected to the timing of avian migratory movement (Erni et al. 2002). The Great Bustard is a diurnal migrant and lacks a uropygial gland, the main function of which is to waterproof the feathers (Jacob and Ziswiler 1982). Snow cover increases the costs of thermoregulation for this ground-roosting species. Additionally, snow cover precludes foraging by the Great Bustard, which depends on dormant vegetation for food in the winter months (Sterbetz

1980, Rocha et al. 2005). Precipitation also obscures the navigation of visual migrants and dampens plumage, hampering flight and increasing thermoregulatory costs. Thus, I predicted that Great Bustards would be less likely to migrate during precipitation events. Research indicates that some bird populations move pre-emptively to avoid advancing storm events, detected through changes in atmospheric pressure, wind, temperature, and cloud cover (Richardson 1990, Newton 2008). Should Great Bustards be similarly sensitive to such indicators, they may migrate in advance of approaching precipitation.

Avian migratory timing is frequently associated with temperature patterns (Richardson 1990). Falling temperatures affect the thermal balance of smaller migrants in particular, but have also been correlated with the movements of larger-bodied birds (Dau 1992). These effects may be indirect, as temperature can be correlated with food availability and wind direction, and change in temperature may be correlated with precipitation (Elkins 1983, Newton 2008). I expected that Great Bustards would move in advance of cold fronts in autumn, which mark the advance of cold fronts and subsequent decrease in quality of forage. In spring, I expected that Great Bustards would migrate on warmer days, which may serve as a signal that resource conditions in northerly breeding grounds are becoming more suitable for breeding.

METHODS

From 2007-2011, 13 female Great Bustards were captured at three leks in northern Mongolia and harnessed with backpack-style 70 g, solar-powered Microwave Telemetry Argos/GPS platform transmitter terminals (PTTs; capture and harnessing described in Kessler et al. 2013). The weight of the PTT was within the recommendations of Kenward (2001) at ≤ 2% of female body weight. PTTs were programmed to collect GPS-quality data every two hours from 0600 to 2000 hrs in spring and fall, and from 0700 to 1900 hrs in winter. The PTTs uploaded these data by radio signal to the Argos satellite system (CLS, Toulouse, France). Tagged birds were monitored until the death of the bird or failure of the transmitter; at time of writing I am still receiving transmissions from one bird (Table 3).

Dates of migration

Spring arrival date was calculated as the ordinal date of the first GPS-quality transmission north of the southern border of the individual bustard's breeding lek in spring. Due to gaps in transmission owing to low battery and radio interference, uncertainty in arrival date was calculated as the duration of time between this transmission and the transmission preceding it. Fall departure date was calculated as the ordinal date of the first GPS-quality transmission south of the southern border of the individual bustard's breeding lek in fall, and uncertainty in departure date was calculated like that of spring. Similarly, arrival and departure from wintering grounds were determined as the first and last day, respectively, on which the bird transmitted from south of the northern boundary of the wintering grounds. Arrival and departure dates with a large degree of uncertainty (>30 days) were dropped from the study (n=3). Because bustards were tagged on the breeding grounds and all mortalities were recorded on migratory stopovers and wintering grounds, more fall departure dates were recorded than spring arrival dates. Duration of migration was calculated as the average of the shortest possible number of days in which the bird could have made the trip (spanning from the latest possible departure date until the earliest possible arrival date for that bird in that year) to the longest possible number of days in which the bird may have made the trip (earliest possible departure date until the latest possible arrival date).

Weather and migratory movements

To test the correspondence between weather patterns and migratory movements, I identified pairs of datapoints collected less than 24 hours apart showing a movement of 40 km or greater, including initial movements from both wintering and breeding grounds (Table 3). This distance excludes movements that fall within the diameter of the maximum breadth of breeding home range I recorded within my sample. Southbound and northbound migratory movements were analyzed separately.

To compare weather conditions on days of departure against recent weather conditions available to the individual bustards, I used a binomial logistic regression. As "positive" departure conditions, I used weather variables at the time and location coordinates at which bustards departed on a migratory movement. To represent weather conditions under which the bustards chose not to migrate (“negative” departure conditions), I created “false” departure datapoints for the days previous to a departure at a specific location. Given the two month average duration of the Asian Great Bustard migration, a period of ten days was chosen as the time frame in which a bustard was plausibly awaiting appropriate conditions for movement.

I used the MoveBank Env-DATA system (Dodge et al. 2013) to annotate environmental data to the true and false departure points. I used mean sea level pressure, snow depth, wind U and V components at 10 m above ground, and total precipitation data from the European Centre for Medium-Range Weather Forecasts Global Reanalysis, reported at six-hour temporal and 0.7° spatial resolution, interpolated bilinearly to the time and location of each datapoint (Appendix A). Arctic Oscillation Index values were interpolated temporally from global values calculated by the National Oceanic and Atmospheric Administration. Given the wind U and V components, I further calculated wind speed and crosswind (following Safi et al. 2013).

As a conservative measure of the ability of Great Bustards to avoid advancing weather conditions, I calculated the change in each weather variable from the day of departure to the subsequent day. Should I have searched for weather shifts within a longer time window, interpretation of positive correlations would have been more ambiguous. As a measure of the response of Great Bustards to recent weather conditions, I calculated the variance of each weather variable in the days preceding departure (Appendix A). As Allen et al. (1996) observed migratory movements of nine species of raptor to peak within 96 hours of the passage of a weather front, four days was chosen as the time period over which to examine variation in weather conditions.

I evaluated a binomial generalized additive mixed model using the gamm4 package (Wood and Scheipl 2014) in R (version 3.1.2) using individual bird as a random effect. gamm4 is currently the only model type to allow both random effects and smoothing parameters. Time and location are significantly correlated in this dataset (MANOVA, $F(2, 1466)=54.2$, $p<0.0001$), and I incorporated a smoothing term to account for spatial and temporal autocorrelation. Incorporation of an additional smoothing term to explicitly address time raised the AIC value. Both autocorrelation terms were statistically insignificant in both northbound and southbound models. Model selection was performed manually using Akaike's Information Criterion. Before running the model, I checked for correlation between weather variables using Pearson and Spearman correlation coefficients. All environmental data were centered and scaled by their standard deviation for modeling.

RESULTS

Dates of migration

The mean date of first transmission at the breeding ground was 22 May. Arrivals were spread over 42 days, from 5 May to 16 Jun (Figure 6a). For individuals for which more than one arrival date was recorded, variation in arrival date from year to year ranged from 3 to 27 days. There was a significant trend toward earlier arrival in each subsequent year that an individual bustard was tracked (Figure 7a; linear mixed-effects model; t_{10}=-5.05, p=0.0005). Mean date of first autumn transmission outside of the breeding ground was 8 Oct. Departures were spread over 99 days, from 31 Jul to 16 Nov (Figure 6b). Among individuals for which more than one departure date was recorded, variation ranged from 2 to 79 days.

Mean date of first transmission at the wintering grounds was 25 Nov. Arrivals were spread over 55 days, from 29 Oct to 23 Dec (Figure 6d). For bustards for which more than one winter arrival was recorded, variation in arrival date from year to year ranged from 9 to 50 days. Mean date of first spring transmission outside of the wintering grounds was 25 Mar (Figure 6c). Departures were spread over 39 days, from 12 Mar to 20 Apr. For bustards for which more than one spring departure was recorded, variation in departure date ranged from 7 to 12 days. I observed a non-significant trend toward earlier departure from wintering grounds in each subsequent spring the bird was monitored (Figure 7b; linear mixed-effects model; t13=-1.58, p=0.16).

In 13 cases, for six individual birds, I was able to determine the duration of a complete spring migration (Figure 8a). These values varied from 28 to 81 days, with an average of 52±13 days. For individuals for which more than one value was available, difference in duration of spring migration ranged from 9 to 15 days. In 19 cases, for seven individual birds, I was able to determine the duration of a complete fall migration (Figure 8b), which averaged 48±32 days. Remarkably, one bird accomplished her fall migration in a period between one and eight days (incorporating the window of uncertainty due to lack of transmission), and a second individual in less than 9 days. The longest journey was completed in 133 days. There was also a wide spread in the fall migration duration of individual birds from year to year, with intra-annual differences ranging from 8 to 99 days.

The range of durations in which fall migration was completed was more than twice that of the range of durations observed for spring migration, but there was not a significant difference in variance of values of duration of migration between the two seasons (F test for equality of variance; F=0.40, df=18, 16, p=0.062). There was also no significant difference in duration of migration in spring versus fall (linear mixed-effects model, t36=0.89, p=0.38). Variance in mean arrival or departure date of individuals did not vary significantly by season (Bartlett's test; K^2=5.8, df=3, p=0.12). However, variance in the range of dates of arrival or departure for individuals monitored over multiple years did vary significantly between season (Bartlett's test; K^2=12.1, df=3, p=0.007), with the most variation observed in departure date from the breeding ground, and the least in departure date from the wintering ground.

Weather and migratory movements

136 departure points from eight individual bustards fit the criteria for analysis for the southbound analysis, and 168 points from six individual bustards fit for the northbound analysis. The minimum AIC model for southbound data included wind support, temperature, change in temperature after departure, and the variability of snow depth in days preceding departure (Appendix B). Bustards were significantly more likely to depart on their southbound journey under favorable wind support conditions (Table 4; Figure 9a; estimate=0.37, p<0.0001), in cooler temperatures (estimate=-0.52, p<0.0001), and on a day preceding a decrease in temperature (estimate=-0.52, p<0.0001) and crosswind (estimate=-0.30, p<0.001).

The minimum AIC model for northbound data included change in wind support after departure, temperature, change in air pressure after departure, variability in the Arctic Oscillation index in days preceding departure, and crosswind (Appendix C). Bustards were significantly more likely to depart on their northbound journey on the day preceding a decrease in wind support (Table 5; Figure 9b; estimate=-0.41, p<0.0001), in warmer temperatures (estimate=0.41, p<0.0001), on days preceding a decrease in atmospheric pressure (estimate=-0.48, p<0.0001), on days preceded by stability in the Arctic Oscillation index (estimate=-0.23, *p*=0.012), and on days preceding precipitation (estimate=0.17, *p*=0.038).

DISCUSSION

Control of migration phenology and timing of migration

I observed a high degree of intra-individual variation in the timing of arrival to and departure from breeding and wintering grounds. High-resolution, longitudinal studies for comparison are rare, but the data that are available indicate a range of consistency in migratory timing between species, with some species showing high consistency (e.g. within approximately five days; (Vardanis et al. 2011, Conklin et al. 2013, Gill et al. 2014), while the timing of others is less repeatable (e.g. within 25 days; Alerstam et al. 2006, Thorup et al. 2013). The degree of intra-individual variation in migration I observed (e.g. 27 days for arrival at the breeding ground; 79 days for departure from the breeding ground; 50 days for arrival at the wintering ground) makes a compelling case for a significant role of plasticity in timing of Asian Great Bustard movement. I observed the least variance between departure dates of individuals monitored over multiple years in spring departure from the wintering ground (12 days), suggesting that endogenous cues may act most strongly at this time.

Studies based on observations at the breeding grounds encounter difficulty in clarifying whether advances in spring arrival are achieved via early departure from the wintering grounds or shortened duration of migration. I observed a significant trend toward earlier spring arrival at the breeding grounds alongside a non-significant trend toward earlier departure from the wintering grounds with each subsequent year a bird was monitored, independent of the arrival of other tagged birds in the same season. No trend was noted in the duration of migration. Together, these findings suggest that individuals arrive at the breeding grounds earlier due to an early departure from the wintering grounds, rather than from a higher migration speed. As studies have documented that early arrival is beneficial for successful breeding (Tryjanowski et al. 2004), these findings may indicate an additional degree of plasticity attributable to learning experience, with younger birds more reliant on endogenous cues (Tøttrup et al. 2010).

Although other studies have found arrival date at breeding grounds to be correlated with conditions at the wintering grounds (Saino et al. 2004), this is unlikely to be an important explanatory factor in this case. All monitored bustards overwintered in the same region, where forage is generally abundant in the form of large territories of irrigated agriculture. If snow cover or late frosts produce interannual variation in resource availability, I would expect to see bustards tracked simultaneously exhibit similar delays or advances in departure from the wintering grounds in comparison to their departure in the previous year. However, the limited simultaneous data available do not display such similarities, and I also observed high intra-annual variation in departure and arrival dates. It is possible that weather and forage conditions along the migratory route may explain some of the variation observed in duration of migration (Balbontín et al. 2009), as each bustard migrated independently and migratory routes diverged by up to 450 km from east to west.

The wide spread in fall departure dates from breeding grounds and fall migration duration may indicate variance in physiological readiness dependent on recent reproductive activity. Great Bustards in these populations experience reproductive failure due to crushing of eggs and chicks by agricultural machinery, predation and severe weather events. The production of two clutches is not unusual. It is worth noting that the latest departure from the breeding grounds was performed by the only bustard observed to have fledged chicks. Great Bustards remain with their mothers for approximately a year, and I observed this individual with these chicks at the migratory staging grounds. At that time they were not able to fly long distances, and it is likely that the mother’s late departure allowed the chicks to gain size and strength for the long migration ahead.

Two female bustards accomplished the 2000 km southbound journey in from one to nine days. In comparison, the average time taken was about twelve times longer, and the most prolonged journey was 20 times as long. It is possible that southbound bustards are not time-constrained, but will use advantageous weather conditions or avoid deleterious conditions when they arise. Data from diurnal non-passerines migrating by flapping flight are scarce, but studies of passerines and shorebirds typically find spring migration to be of shorter duration than fall migration (Newton 2008, Yohannes et al. 2009). I observed the opposite in Great Bustards, which may migrate faster due to wind support from the Siberian Anticyclone in fall. In spring, migrants moving north into the severe Central Asian climate may move slowly as they encounter steep environmental gradients (Raess 2008). As long-distance migrants, it is also possible that Great Bustards pursue a "wait and see" strategy in spring, pausing at each stopover until environmental cues indicate that conditions to the north are suitable (Tøttrup et al. 2010, Gunnarsson and Tómasson 2011, Sawyer and Kauffman 2011). Long stopovers in spring may also serve as a mechanism to accumulate resources for breeding upon arrival at the lek.

Weather and migration

In spring, female Asian Great Bustards were significantly more likely to make migratory movements on days preceding a decrease in atmospheric pressure and on days preceding precipitation. These findings are consistent with those of Alerstam (1990) regarding the northbound migration of European birds in the days preceding a cyclone. These findings can be attributed to an avoidance of migrating in wet weather, particularly for Great Bustards, which lack a uropygial gland and thus have limited plumage protection from rain.

Wind support plays the largest role in determining the energetic costs of migration (Pennycuick 1989), and Asian Great Bustards were significantly more likely to depart on their northbound journey on the day preceding a decrease in wind support, as well as significantly more likely to make a southbound movement when wind support was greater. It is not clear why these bustards were more likely to make southbound movements on days preceding a decrease in crosswind. As larger birds, Great Bustards are more buffered from the effects of wind than lighter birds (Pennycuick 1969). Kessler et al. (2013) observed considerable east-to-west spread in migratory route and stopovers of individual Asian Great Bustards from year to year; this may be the effect of flight under conditions of crosswind.

I observed that female Asian Great Bustards were more likely to migrate on warmer spring days and cooler autumn days. It is often taken as common knowledge that temperature plays a key role in determining the timing of bird migration (Richardson 1990), but whether the effect is direct or indirect (e.g. through temperature's correlation with vegetation productivity) is uncertain (Newton 2008, Lehikoinen and Sparks 2010). Due to large-scale autocorrelation in weather systems, warmer temperatures on stopovers in spring may be associated with more favorable conditions on the breeding grounds. It is likely that cooler temperatures in autumn presage advancing winter weather.

Conservation implications

Great Bustard populations have disappeared from much of their Eurasian range, and remaining populations are typically fragmented, declining, and under increasing threat (BirdLife International 2001, Alonso and Palacín 2010). An understanding of the migratory response of this species to altered climate conditions can not only aid in prioritization of conservation actions for endangered populations, but also in choice of appropriate stock for reintroduction programs in areas where the species has been extirpated (e.g., Great Britain; Waters and Waters 2005, Hall 2012). The wide variation in migratory timing, and correlation between environmental cues and migratory behavior described above, may indicate that Asian Great Bustards are better-equipped to cope with changes in climate conditions across the migratory range than species with stricter endogenous control of migratory phenology based on photoperiod (Both and Visser 2001, Coppack and Both 2002).

Over the second half of the 20^{th} century, air temperatures in the breeding range of the Asian Great Bustard have risen faster than in most regions of the globe, particularly in winter (Batima et al. 2005, Dagvadorj et al. 2009). The average duration of winter cold spells has decreased by almost two weeks, alongside a decrease in the strength of the Siberian Anticyclone

(Gong and Ho 2002, Batima et al. 2005). Tendencies towards earlier onset of first snow in autumn, increasing winter snowfall, later appearance of the final snow cover in late spring or early summer, and decreasing summer rain have been observed (Batima et al. 2005, Dagvadorj et al. 2009). Temperature, dryness, and desertification are also expected to increase at bustard stopover sites in Nei Mongol, China (Wang et al. 2009).

Given the results of my modeling, which show greater likelihood of southbound migratory movement under conditions of favorable wind support and cool or decreasing temperature, it seems likely that Asian Great Bustards may extend their tenure at breeding grounds under a climate change conditions involving a weakened Siberian Anticyclone and moderate autumn temperatures. Such behavior would be consistent with that of other late-season migrants (Miholcsa et al. 2009). This delay could potentially increase the reproductive rate of these populations by allowing for greater success of replacement clutches (Møller et al. 2010), which have been observed in these populations after a first clutch is lost (Kessler, unpublished data). However, weakening of the Siberian Anticyclone would reduce tailwinds for the fall journey and thus increase its energetic cost, which may result in increased mortality as the Gobi desert widens (Wang et al. 2008, Lok et al. 2015).

Rising spring temperatures due to climate change may result in the early arrival of Asian Great Bustards at the breeding grounds. However, as Great Bustards are capital breeders (Stephens et al. 2009), nesting upon arrival at the lek using stores of body fat, it is likely that clutches will be lost if the trend toward late snowstorms resulting in lasting snow cover continues. Late spring snow cover and early autumn snowfall may mean that farmers are unable to extend the agricultural season and that the current planting schedule persists, despite rising temperatures. In this case, loss of eggs and chicks due to crushing by farm machinery are likely to continue. In a study of over 400 species, Hockey et al. (2011) found that migrants were more likely to have expanded their ranges into cooler regions over the past thirty years. It is uncertain whether Great Bustards will be able to shift their breeding range northwards as summer temperatures increase. Though I have documented responsiveness to weather cues, and this species is sensitive to summer heat (Morales et al. 2006, Alonso et al. 2009), as lekking species, Great Bustards display a high level of philopatry to their breeding sites (Alonso et al. 2004).

I found that Asian Great Bustards spend on average approximately one-third of the year on migration, making stopover quality and threats along the migratory pathway of great importance to the conservation of this subspecies. If key migratory stopovers in the Gobi Desert are affected by continued desertification, mortality of Great Bustards on the migratory journey may rise. The duration of the spring migratory journey may also increase as bustards spend prolonged periods refueling at sites with reduced productivity (Both 2010). Female Asian Great Bustards spend an additional third of the year moving nomadically over large territories. Though they are not philopatric to specific wintering ranges from year to year (Kessler et al. 2013), all winter territories observed within the tagged sample are within a single 200 km agricultural plain in southern Shaanxi Province, China. It is unclear whether the correlations between temperature and migratory movement in Asian Great Bustards, combined with increasing winter temperatures across northern Asia could result in a shift in the overwintering location of these populations (Visser et al. 2009).

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Table 3. Dates of transmission and number of datapoints used for modeling for each Asian Great Bustards monitored.

			Number of Migratory Movements Used for Modeling	
Bustard Name	**First Transmission**	**Final Transmission**	**Southbound**	**Northbound**
Nergui	Jun-07	Rarely Receiving	6	5
Dolgoon	Aug-07	Nov-07	0	0
Songuul	Jun-08	Mar-11	17	29
Ulaana	Jun-08	Dec-09	9	2
Nomin	Jul-08	Nov-08	1	0
Sondor	Sep-08	Oct-08	0	0
Tsashan	Oct-08	Dec-08	5	0
Mongoljin	Oct-08	Nov-08	0	0
Tsengel	Aug-09	Dec-09	7	0
Toson	Sep-09	Oct-10	4	6
Sachokchin	Sep-10	Currently Receiving	24	66
Mendee	Jun-11	Nov-14	62	60
Bosoo	Jun-11	Nov-11	0	0
Total:			135	168

Table 4. Parameter estimates of the model with minimum AIC, analyzing relationship between weather variables and southbound migratory movements of Asian Great Bustards.

	Estimate	**Standard Error**	**z-value**	***p***
Intercept	-2.53	0.11	-23.56	<0.0001
WindSupport	0.37	0.089	4.20	<0.0001
Temp	-0.52	0.11	-4.87	<0.0001
ChangeTemp	-0.32	0.094	-3.38	<0.0001
ChangeCrosswind	-0.30	0.092	-3.29	<0.001
SD4DaysSnowDepth	-0.18	0.11	-1.58	0.11

Table 5. Parameter estimates of the model with minimum AIC, analyzing relationship between weather variables and northbound migratory movements of Asian Great Bustards.

	Estimate	Standard Error	z-value	*p*
Intercept	-2.54	0.098	-25.88	<0.0001
ChangeWindSupport	-0.41	0.085	-4.74	<0.0001
Temp	0.41	0.087	4.72	<0.0001
ChangeAirPressure	-0.48	0.098	-4.92	<0.0001
SD4DaysArcticIndex	-0.23	0.093	-2.52	0.012
ChangePrecip	0.17	0.080	2.08	0.038
Crosswind	0.13	0.088	1.52	0.128

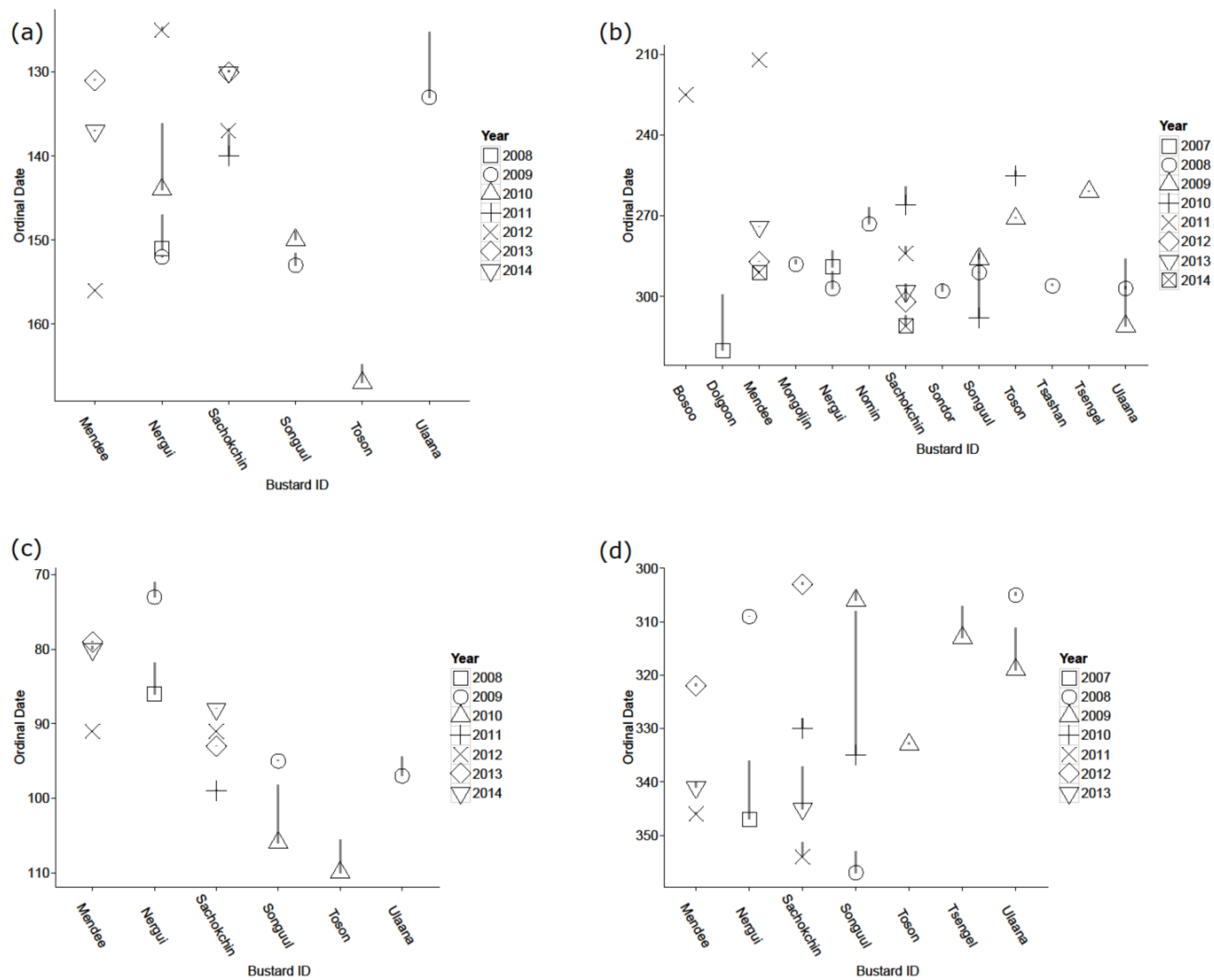

Figure 6. Timing of migration for individual Asian Great Bustards: (a) spring arrival date to breeding lek; (b) fall departure date from breeding lek; (c) spring departure date from wintering grounds; (d) fall arrival to wintering grounds. Shape represents year of observation. Length of attached bar indicates period of uncertainty during which the bird may have arrived or departed.

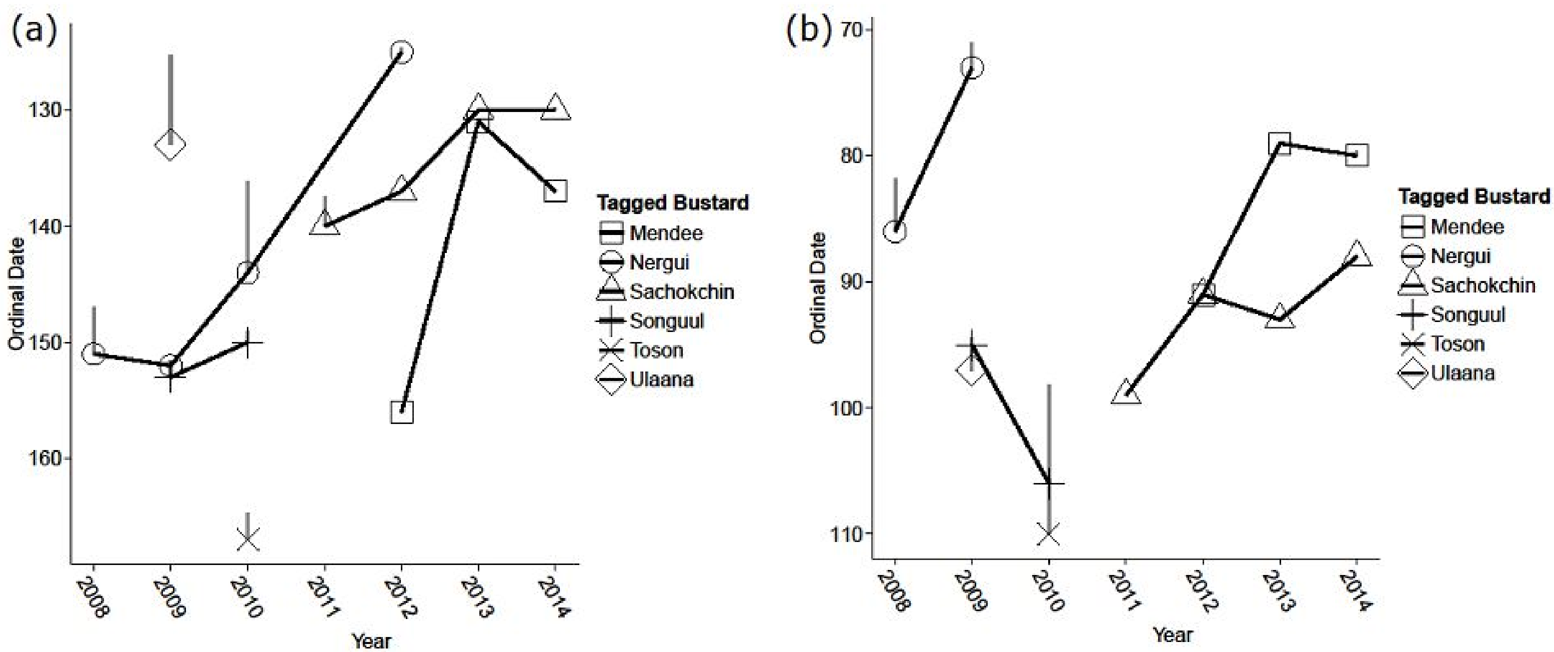

Figure 7. Arrival at breeding grounds (a) and departure from wintering grounds (b) by year. Shape represents individual Asian Great Bustard observed. There is a significant trend toward earlier arrival at breeding grounds in each subsequent year an individual bustard was monitored (linear mixed-effects model; $t10=-5.05$, $p=0.0005$) There is a non-significant trend towards earlier departure in each subsequent year an individual bustard was monitored (linear mixed-effects model; $t13=-1.58$, $p=0.16$).

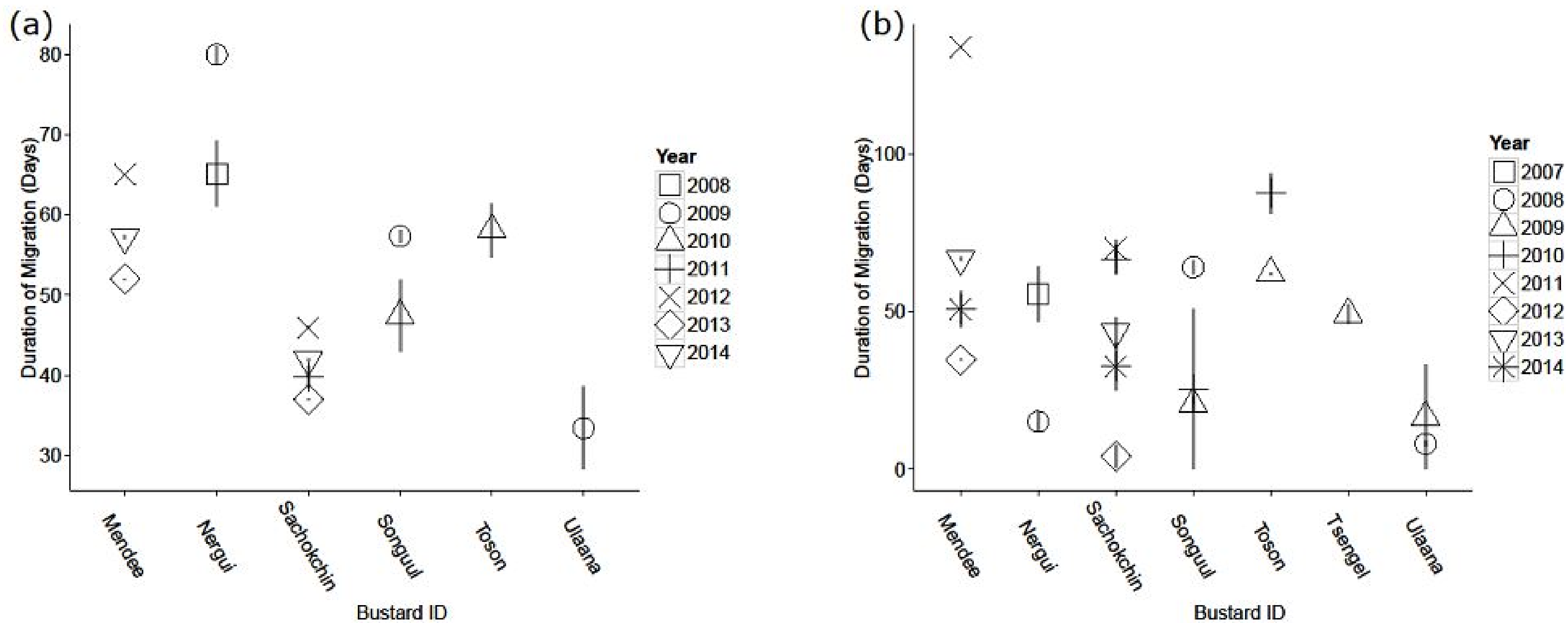

Figure 8. Duration of (a) spring and (b) fall migration by year for individual Asian Great Bustards. Shape represents year of observation. Length of attached bars indicates period of uncertainty in cases of poor transmission.

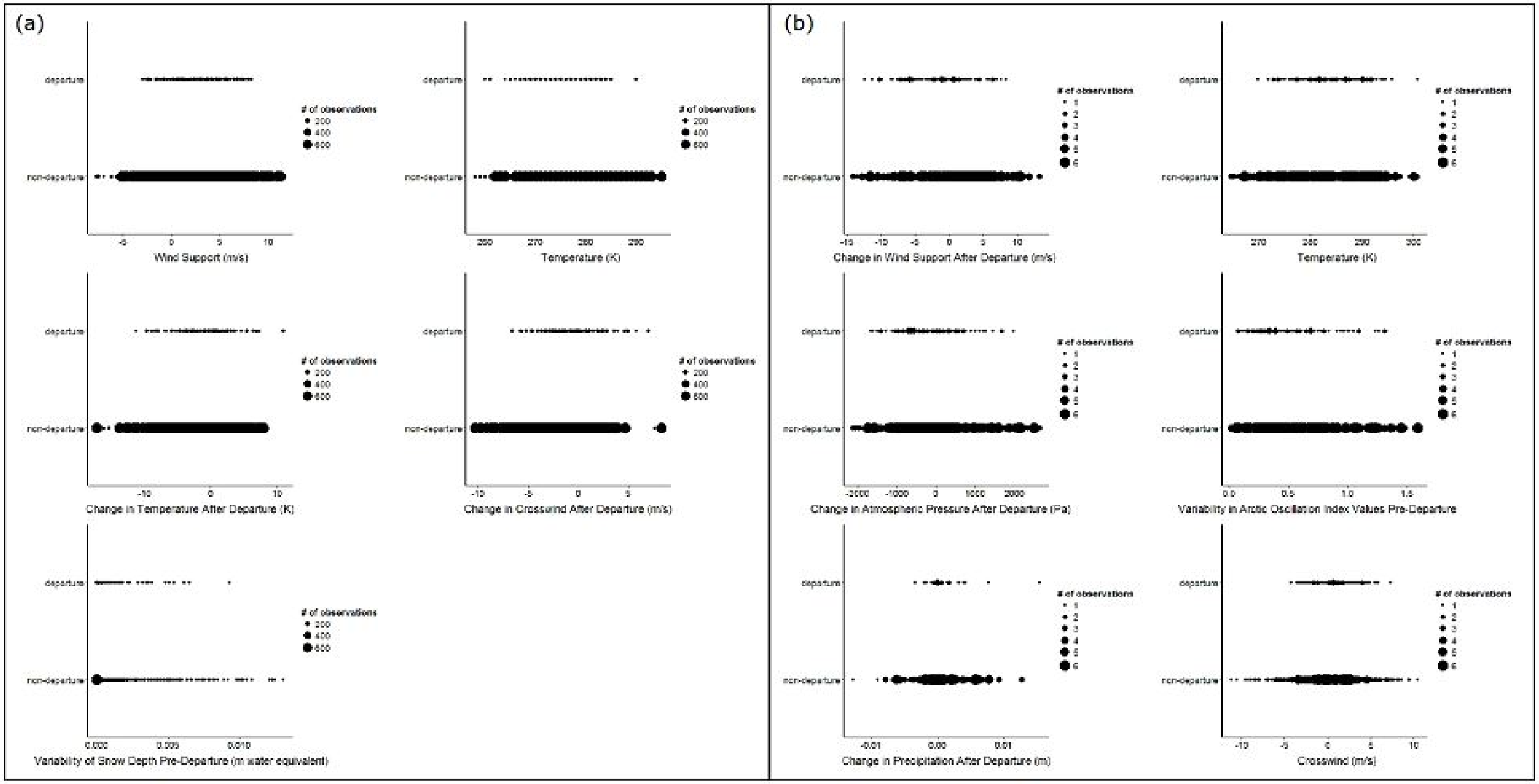

Figure 9. Weather predictors included in the top model characterizing (a) southbound; and (b) northbound migratory movements of Asian Great Bustards. For southbound movements, wind support, temperature, change in temperature, and change in crosswind are significant predictors with p-values <0.001. For northbound movements, change in wind support, temperature, and change in air pressure were significant predictors with p<0.0001.

CHAPTER 4

HABITAT USE OF ASIAN GREAT BUSTARDS (OTIS TARDA DYBOWSKII) IN AN AGRICULTURAL MOSAIC

ABSTRACT

Though the Great Bustard (*Otis tarda*) originated as a grassland species, today this species is dependent on agricultural habitat across the western portion of its vast Eurasian range. In Central and eastern Asia, where natural steppe habitat is still available, reports of Great Bustard describe the use of both natural and human-modified habitats. Clarification of the habitat use patterns of the endangered Asian subspecies (*O. t. dybowskii*) is urgently required to inform conservation measures. Five Asian Great Bustards were captured at a lek in northern Mongolia and fitted with backpack-style GPS-satellite transmitters to monitor their movements throughout the breeding season. High-resolution satellite imagery was used to map habitat availability at the lek, including shifts in agricultural field status over the years in which the bustards were monitored. Female Asian Great Bustards used pasture and wheat agriculture at approximately the same frequency, though the availability of pasture was higher. Female Asian Great Bustards used forest habitat in a small but notable measure, and the majority of nests were within 100 m of a forest edge. In no habitat type was a chick successfully fledged. The single male Great Bustard monitored showed fidelity to the lek center, which resulted in a shift in his habitat use patterns from one year to the next, as agricultural fields were converted from wheat to fallow. Within the research site a trend toward conversion of abandoned agricultural lands to active production was noted. As agricultural production expands across the range of the Asian Great Bustard, compatible management practices should be promoted at both the landscape and field level.

INTRODUCTION

The Asian subspecies of Great Bustard (*Otis tarda dybowskii*) is of conservation concern, with only approximately 2000 individuals remaining in Siberian Russia, Mongolia and China. An understanding of the habitat requirements of this subspecies is required to inform conservation management.

The bustard family (Otididae) likely originated in east and southern Africa, and most species today are residents of similar dry grassland or desert habitats (Johnsgard 1991, Collar 1996, Pitra et al. 2002, Broders et al. 2003). Great Bustards are historically inhabitants of the Eurasian steppe, a vast expanse of grassland stretching from Hungary through eastern Siberia. The range of the European subspecies (*O. t. tarda*) expanded into Europe as forests were felled for agriculture in Middle Ages (Isakov 1974).

Levshin (1813) described an analogous transition from steppe to agricultural habitat for Great Bustards in European Russia as beginning in the 18th century. The largest contemporary population of Great Bustards in Russia is found along the lower Volga River, in an agricultural mosaic composed primarily of wheat farmed with fallow rotations, interspersed with pasture and hayfield (Gabuzov 2000, Khrustov 2009, Oparin et al. 2013).

The survival of European populations is now highly to completely dependent on the compatible management of these anthropogenic ‘cereal steppes,’ (Flint 2000, Faragó et al. 2001, Moreira et al. 2004, Pinto et al. 2005). However, the habitat requirements of Great Bustards in the eastern portion of its range, where large tracts of natural steppe habitat are still available, are less well understood.

Writing during a time of explosive agricultural growth in northern Kazakhstan, Ryabov (1949) found Great Bustards already using fallow fields preferentially to open steppe, but never sighted them on planted fields. Today, Gubin (2007) describes Great Bustard populations in Kazakhstan and the Central Asian states as displaying ecological plasticity in their use of both natural steppe and human-modified agricultural habitats. Environments used by this species in the broader central Eurasian region today includes both forest and open steppe, flooded river plains and dry steppe with sparse vegetation, and agricultural collectives (Irisova 2008, Nefedov 2013).

In east Asia, the endangered Asian subspecies (*O. t. dybowskii*) uses both steppe and forest steppe habitat (Elaev 2013). Some populations are described as having adapted to agricultural fields and fallows, while others inhabit virgin steppe, moist meadows and watercourses (Tseveenmyadag 2001, Batsaikhan 2002, Popov and Medvedev 2010). A defining feature of the Asian subspecies may be its tolerance for forest. While the western subspecies generally avoids forest and requires open vistas, some Asian populations undertake long-distance flights over taiga to reach isolated forest clearings (Ponomareva 1986, Goroshko 2008).

The goal of this research is to clarify the habitat use patterns of the Asian Great Bustard in northern Mongolia, one of their population strongholds (Boldbaatar 1997). As Mongolia expands its wheat production (Regdel et al. 2012), it is important to understand the degree to which these birds rely on agricultural fields with the aim of developing conservation recommendations for agricultural practices compatible with conservation of this vulnerable subspecies.

METHODS

One male and four female Great Bustards were captured at a lek in an agricultural valley in northern Mongolia and harnessed with backpack-style 70g, solar-powered Argos/GPS platform transmitter terminals (PTTs, Microwave Telemetry, Columbia, USA) as described in (Kessler et al. 2013). The weight of a PTT represents less than 2% of the body weight of a female Great Bustard, within the recommendations of Kenward (2001). PTTs collected GPS-quality location data every two hours from 6:00 to 20:00 during spring and fall, and from 4:00 to 22:00 in summer. Those data were then uploaded by radio signal to the Argos satellite system (CLS, Toulouse, France), though successful transmission was sometimes limited by battery charge and radio interference. Data were collected until the death of the bird or failure of the transmitter. Data from individuals in flight were excluded from this analysis of habitat-use patterns.

Great Bustard eggs are incubated for 25 to 28 days (Johnsgard 1991, Kapranova et al. 2004), but clutches and incubating females are frequently crushed by farm machinery and lost to aerial and terrestrial predators (Ryabov 1949, Demeter et al. 1994, Watzke 2007, Spitsin 2008). To identify nesting attempts of even short duration, I identified all locations at which the bustard was recorded three or more times. When possible during field work, the subsequent reproductive status of the female was confirmed through visual observations. When in-person observation was not possible, I evaluated the movement patterns of the bustard (speed, frequency of movement, and distance moved) for compatibility with incubation and the lesser mobility of chicks (Osborne and Osborne 1998).

Study area

The minimum convex polygon describing the movements of all tagged bustards within the mountain-ringed valley containing the Great Bustard lek was defined as the area of study (approximately 50°N, 101°E). The area of study is located in forest steppe in the transition zone between Mongolian steppe and East Siberian taiga (Hilbig 1995, Anenkhonov et al. 2008). This ecotonal community exhibits a sharp delineation between forest and steppe, with forest typically found on shadier northern slopes and steppe vegetation on southern slopes and in valleys.

The central portion of the area of study consists of a valley at 1100 meters above sea level which is dominated by low-intensity, dryland agriculture, almost exclusively summer wheat (*Triticum spp.*) grown in moderately sized fields . Small plots of potatoes (*Solanum tuberosum*) are cultivated for personal use. Fallow fields are often overgrown with *Artemisia spp. b*etween plowing, as are abandoned fields. Grassland around and between agricultural fields is cut for hay. Grassland composition is typical of the mountain and forest steppe belt in this region, with forage consisting of species in the genera *Carex*, *Artemisia*, *Oxytropis*, *Potentilla*, *Poa* and *Allium* (Ariuntsetseg 2006, Sandanov 2007, Ganbold 2010, Kakinuma and Takatsuki 2012).

The valley is roughly 20 km along the major axis and 10 km along the minor axis, and is ringed by forested mountains up to 1900 meters in altitude. Forests are predominantly larch (*Larix sibirica*) mixed with pine (*Pinus silvestris*) and spruce (*Picea obovata*). Birch (*Betula pendula*)-aspen (*Populus tremula*) forests are common at lower elevations and Siberian stone pine (*Pinus sibirica*) at higher elevations (Sandanov 2007). A large, braided river with forested islands and banks runs along the east side of the valley.

The county seat is located in the southwest corner of the area of study and seasonally fluctuates in population from 500 to 2500 individuals. The entire valley, including grassland, fallow, and agricultural stubble is used for winter grazing of sheep (*Ovis aries*), goats (*Capra* *aegagrus hircus*), cattle (*Bos taurus*), horses (*Equus ferus caballus*), and yak (*Bos grunniens*) by a pastoral nomad community outside of the agricultural season.

Habitat categorization

Habitat in the valley was classified as forest, virgin pasture, abandoned fields, fallow fields, and active fields for each of the years of study. IKONOS-2 satellite imagery (Digital Globe, Longmont, USA) with 0.8 m resolution was used to delineate the boundaries of forests, rivers, and fields. This level of resolution is sufficient to identify individual trees and head of livestock. Tree stands and rivers were detected and outlined using object-oriented classification algorithms in Definiens eCognition (Benz et al. 2004), Version 9.0, Trimble, München, Germany) and verified by eye. Individual fields were outlined manually.

In any particular year, fields in this region may be actively farmed with wheat or vegetables, plowed as fallow in preparation for planting in one or two years, or abandoned (unworked). Each of these field types exhibits a different phenological sequence due to the differential presence or absence, and timing, of plowing, mowing and harvesting activities (de Beurs and Henebry 2004). Field status in each year of the study was determined through comparison of Poaceae Abundance Index values (Shimada et al. 2012) calculated from Landsat satellite imagery (United States Geological Survey, Reston, USA) with 15 m panchromatic and 30 m multispectral resolution from each month of the growing and harvest season (May through October). Field status was then verified through comparison to photographs taken from established vantage points during each year of field research.

Statistical calculations

Area and overlay operations were carried out in ArcGIS 10.2.2 (Esri, Redwoods, USA). Statistical comparisons and modeling were carried out in R (version 3.1.2) including the lme4 package (Bates 2010). The adehabitatHS package (Calenge 2011) was used for compositional analysis of habitat use (Aebischer et al. 1993). The analysis was carried out once with data from all birds, and once with data from only female birds in order to parse out the effect of adding data from the male.

As neither the number of years a bustard was observed, nor the number of observations per bustard in each year was consistent, I treated each individual as a single replicate for modeling and graphing. Thus when multiple years of data were recorded for a single bird, I averaged those data to obtain a single value for that individual. As the Great Bustard is a species of open landscapes, the percentage of each habitat type available was calculated from the sum total of open habitat types in the area of study, excluding interior forest habitat.

RESULTS

Agricultural trends

Most fields in the valley are treated with a two-year rotation, planted with summer wheat in one year and plowed as fallow in the subsequent year. The territory allotted to fallow and wheat are roughly equal in each year (Figure 10). Farm managers have clustered active and fallow fields together to minimize the movement of agricultural machinery. Thus, in odd years the southern valley is planted and the western valley fallow, and vice versa in even years. A noteworthy change to this system occurred in 2013, when wheat-fallow-strip farming was introduced on two of the largest, central fields of the valley. There is also a trend toward the reclamation of abandoned farmland (Figure 10).

Telemetry data

The number of locations collected for each bird during each breeding season ranged from 23 to 1051, dependent on battery charge and radio interference (Table 6). The male bustard (Bayan) displayed at this lek but also visited neighboring leks in other valleys, with the result that less data was collected from this bird. All deaths occurred outside of the breeding area.

Habitat use

Female habitat use differed significantly between habitat types (Figure 11; ANOVA, $F_{5,18}$=18.45, p<0.0001). However, a post-hoc Tukey test showed no significant difference in use between wheat field phenologies (fallow, actively planted with wheat, and abandoned; all p values>0.6) , and I combined these categories for further analysis. In this reduced analysis, comparing use of pasture to use of all wheat fields, forest and vegetable fields, habitat use differed significantly (Figure 12; $F_{3,12}$=43.45, p<0.00001). A post hoc Tukey test showed no significant difference between pasture and combined wheat agriculture (p=0.12), indicating that females spend approximately the same amount of time in pasture and in wheat agriculture habitat.

In contrast, almost twice as many observations of the male great bustard were in wheat agriculture areas than in pasture (Figure 11). The male's use of planted as opposed to fallow agricultural fields varied greatly between years (Figures 13 & 14).

To test whether these differences reflect a habitat preference or simply the availability of habitat types in the environment, I performed a compositional analysis of habitat use. Because of difficulty testing the normality of data given the small sample sizes (n=5 and n=4), I performed the test with both parametric and non-parametric (randomization) methods. This test indicated that bustard locations in wheat agriculture were over-represented compared to the availability of this habitat type in the environment, though this result may have been driven by data from the male bustard (Table 7, Figure 14).

As described in "Agricultural Trends," two large-scale habitat configurations are observed in the agricultural mosaic - one in which the southern valley is planted and western is fallow and vice versa. Thus, if Great Bustards are highly philopatric to a specific home range during the breeding season, I expected to see a difference in habitat use in odd years and even years. A weak biannual alteration between observations in wheat and fallow fields can be discerned for individual bustards (Figure 13). However, inclusion of a "valley configuration" term in a linear mixed-effects model describing habitat use increases the AIC value, and is statistically indistinguishable from a model without the term (χ^2(6, N=16)=0.51, p=0.99).

A small though consistent number of observations of females occurred within forest habitat (Table 6). The forest frequented by females was adjacent to agricultural fields and pasture. Females did not visit forest adjacent to the large river which runs along the east of the valley. The male was not observed in the forest (Table 6).

Nest sites

Reproductive failure was universal among female Great Bustards in all years they were monitored (Table 8). Though in some cases eggs were successfully hatched, no chicks fledged. In two cases, the female laid a replacement clutch, which also failed. The ratio of nests in agricultural fields to nests in pasture roughly matched the ratio of agricultural fields to pasture in the area of study. Most nests were located within 100 m of a forest edge. There was a high degree of philopatry in choice of nesting locations. All nests of female “Mendee” were located in a 250 m wide valley enclosed by forest at 25 km distance from the lek center, in which there is no agriculture.

DISCUSSION

Asian Great Bustard habitat use

This population of Great Bustards regularly uses both wheat field and pasture habitat. Specifically, the female Asian Great Bustards I observed spent similar amounts of time in wheat agriculture and pasture, however, the availability of pasture is greater in the area of study. The proportion of nests placed within agricultural fields roughly matched the availability of this habitat in the area of study. The male Asian Great Bustard used agricultural fields at roughly twice the rate of pasture. However, the use of agricultural habitat by Asian Great Bustards appears to be less intense than that of European Great Bustards, some populations of which strongly avoid uncultivated areas (Lane et al. 2001, Moreira et al. 2004, Watzke 2007).

Though there are a few records of European Great Bustards using habitat with light tree cover (e.g., Rocha et al. 2013; Lane et al. 1999; Palacín et al. 2012), the western subspecies is typically described as requiring open landscapes (Johnsgard 1991, Nagy 2009). In concordance with Goroshko (2008), this study finds the Asian Great Bustard to be tolerant of dense forest edge. I recorded a small but consistent use of forest habitat by female Great Bustards. These observations are likely an underestimate, as s successful receipt of GPS satellite signals is less likely under canopy cover. Females also frequently used pasture adjacent to forest edge, and the majority of nests were less than 100 m from forest edge. Further, to reach the lek site, Great Bustards must cross from 35 to 200 km of forest. While I observed use of forest adjacent to pasture and agriculture, I did not observe any use of riverside forest, or visits to the valley's large river.

This record of agricultural and forest-edge habitat use by Great Bustards is notable because large tracts of open steppe habitat are still available in Mongolia (Batsaikhan et al. 2014), in contrast to other portions of the species' range. The Great Bustards I monitored migrated annually through hundreds of kilometers of open steppe, the suitability of which they are presumably able to assess during multiple and sometimes lengthy stopovers (Kessler et al. 2013).

While female Great Bustards incubate eggs and raise chicks singly, male Great Bustards continue to display at the lek to gain additional copulations from late-breeding females or females which are producing second clutches (Johnsgard 1994). Observations of the male tagged in this study ("Bayan") were concentrated in the center of the lek in both years he was observed. This resulted in a dramatic change in his habitat usage metrics from one year to the next as those fields were alternated from wheat production to fallow.

Within the lek center, Bayan used agricultural fields more than the surrounding pasture matrix. The uniformity of vegetation (or lack of vegetation) on planted and fallow wheat fields during the lekking season is likely to provide better visual contrast for males' breeding display, which may improve chances of mating (Gray et al. 2007, Olea et al. 2010). Summer plowing of the fallow fields at the center of the lek in 2009 may have forced Bayan to use more of the adjacent pasture habitat than in the previous year.

Role of habitat heterogeneity

The complexity of the agricultural mosaic at my research site may be key to its status as one of the few remaining harbors for this rare subspecies (Fahrig et al. 2011, Wiens 1995). In the valley, management practices and timing of agricultural activities differ in each habitat type, enhancing spatial and temporal heterogeneity. This complexity may be attractive to females seeking resources to both feed and conceal themselves and chicks from predators (Magaña et al. 2010).

Great Bustards are sensitive to human disturbance (Gewalt 1959, Hummel 1985, Collar 1996, Gubin 2007), particularly in the Asian portion of their range where they are more heavily persecuted by hunters (Ponomareva 1986, Goroshko 1999, Tseveenmyadag 2001). At this research site, the presence of wheat agriculture decreases the level of disturbance to Great Bustards during the breeding season in comparison to what would be encountered in unmodified steppe habitat. Due to a ban on livestock in agricultural fields, the valley is not used as summer pasture even when nomadic pastoralists are forced out of their normal summering grounds by drought conditions. For the most part, humans are present in the valley in summer only to carry out agricultural activities, and because of the varied work schedules for fallow as opposed to wheat fields and the limited availability of farm machinery, some portion of the valley is always free of human disturbance.

In addition, agricultural fields provide a refuge for bustards from perceived threats such as approaching humans. The high vegetative growth of untilled fallow and mature wheat provides cover for hiding, the soft soil of tilled fields slows the approach of hunters (as well as researchers attempting to capture bustards!), and a ban on setting foot in active wheat fields precludes human activity altogether.

Reproductive success and nest site selection

The reproductive success of ground-nesting bird species is often depressed by high rates of predation, as is the reproductive success of farmland birds, whose nests risk destruction by agricultural machinery. Correspondingly, Great Bustard reproductive rates are typically low across the species' range. Nest and nestling survival rates of 30% are reported for Asian Great Bustards on Chinese grasslands (Zhao et al. 2006, 2007). Similar or lower rates are reported for the European subspecies (Ena et al. 1987, Demeter et al. 1994, Morales et al. 2002, Watzke 2007).

Over the course of this study, all recorded reproductive attempts failed, regardless of the habitat in which the nest was placed. One of these nests was located in a fallow field and thus may have been destroyed during summer plowing. It is likely that other reproductive attempts succumbed to corvids, raptors, and canids, as in other portions of the species' range (Ryabov 1949, Demeter et al. 1994, Langgemach 2008, Chernobai et al. 2011). The introduction of agricultural fields may have increased corvid density in the valley (Manzer and Hannon 2005). The valley is additionally embedded within a forest matrix, which may increase the rate of predation experienced from Red Foxes (*Vulpes vulpes*). Across Mongolia, Red Foxes are commonly hunted for market trade of pelts (Wingard et al. 2006, Murdoch et al. 2010), but hunter success is likely lower near forest edge than in open steppe.

Over multiple years of field research in this valley, I have observed a low rate of Great Bustard reproduction as judged by the number of fledglings accompanying females during pre-migratory staging. This suggests that the reproductive failures I observed in tagged birds may be typical. However, I cannot exclude the possibility that the attached transmitters decreased the breeding success of female Great Bustards in this study. A meta-analysis has found that transmitters decrease nest success, increase nest abandonment, and decrease the likelihood of nesting, though the effects are small (Barron et al. 2010).

The female Great Bustards monitored spent approximately the same amount of time foraging in wheat fields as in pasture, despite the greater availability of pasture. However, they placed their nests in pasture in approximately the same ratio as this habitat is available in the valley. A similar tendency has been noticed in Hungary (Végvári and Kapocsi 2005). Pastures offer higher levels of arthropod biomass (Litzbarski and Watzke 2007), which may be important for feeding chicks. In this valley, pasture is also associated with reduced human traffic during the summer and agricultural activity.

Females observed in this study also chose nest sites close to forest edge. As forests in this valley cover mountaintops and north-facing slopes, a nest site near a forest edge is also typically situated on a slope, which provides a vantage point to scan for the approach of predators (Magaña et al. 2010). Great Bustards are sensitive to heat (Alonso et al. 2009a) and a forest edge nest site is likely to benefit from the shade of the mountain as well as cool air moving downhill from the forest.

Habitat change and conservation priorities

Though most of Mongolia has a harsh climate and poor soil which are relatively unsuited to agriculture, its northern provinces have been targeted for wheat development, particularly during the last two decades of the communist period (1970-1990; Tian et al. 2014). Many fields were eventually abandoned due to soil degradation, and later economic turmoil and recession following the transition from socialism to a free-market economy (Hirano and Batbileg 2012, Regdel et al. 2012, Baast and van de Fliert 2013). These same economic events resulted in dramatic drops in fertilizer and pesticide use across the region (Gintzburger et al. 2005).

In response to rising global wheat prices, in 2008 Mongolia's legislature introduced the Third Virgin Lands Campaign ("Tselina-3")aimed to increase domestic production of this staple (Regdel et al. 2012). The impacts of this legislation and of Mongolia's economic recovery are seen at this research site in the trend toward reclamation of abandoned farmland. The conversion of virgin steppe to agriculture was not observed over the course of the study.

The findings of this study suggest that the conversion of abandoned fields to active fallow and wheat production may be compatible with Great Bustard conservation. However, intensification of agricultural practices at either the landscape or field scale would be cause for concern. Simplification of the agricultural mosaic through abandonment of fallow rotations for consistent annual wheat production is likely to decrease resources for breeding (Guerrero et al. 2011, 2012, Winqvist et al. 2011). It would also decrease the heterogeneity of the agricultural mosaic, which currently provides resources for divergent male and female Great Bustard habitat requirements.

Even small changes in the rate of female reproductive success of this lekking species are capable of changing extinction probability (Lane and Alonso 2001). At the scale of field management, it is vital that disturbances that may flush breeding females and attract the attention of predators to their eggs and chicks be avoided. This requires that the use of agricultural machinery be minimized during the nesting season.

Though no agricultural chemicals are currently used, there is potential for their adoption as Mongolia's Millennium Road Project is completed and overland transport becomes more cost-efficient. Pesticides decrease the protein-rich insect food base important to Great Bustard summer diet, and vital to fast-growing chicks (Ryabov and Ivanova 1971, Tian et al. 2004, Martín et al. 2007, Alonso et al. 2009b, Bravo et al. 2013). Asian Great Bustard chicks must develop particularly rapidly over the short Mongolian summer before embarking on a long-distance autumn migration (Kessler et al. 2013). Agricultural chemicals have also caused direct mortality to bustards (Puzanskii 2000), as well as long-term effects rendering Great Bustards more susceptible to pathogens and parasites (Lemus et al. 2011) and reducing reproductive success (Oparin et al. 2013).

Outside of Mongolia, the most important population of Asian Great Bustards is found in northeastern China. During the 1990s, almost one million hectares of land in this region were converted to dryland agriculture; the majority of this was grassland (Liu et al. 2005). Given the regular usage of agricultural fields by Asian Great Bustards recorded in this study and the increasing extent of this habitat across their range, emphasis should be placed on the development of agricultural guidelines compatible with both the conservation needs of the Asian Great Bustard and constraints on agriculture in the harsh Central Asian environment. The palatability of these measures to farm managers may be increased with the knowledge that the Great Bustard consumes little grain crop, and performs ecological services by consuming large numbers of agricultural pests during the growing season (Ryabov 1949; Lane et al. 1999; Litzbarski and Watzke 2007; Bravo et al. 2013).

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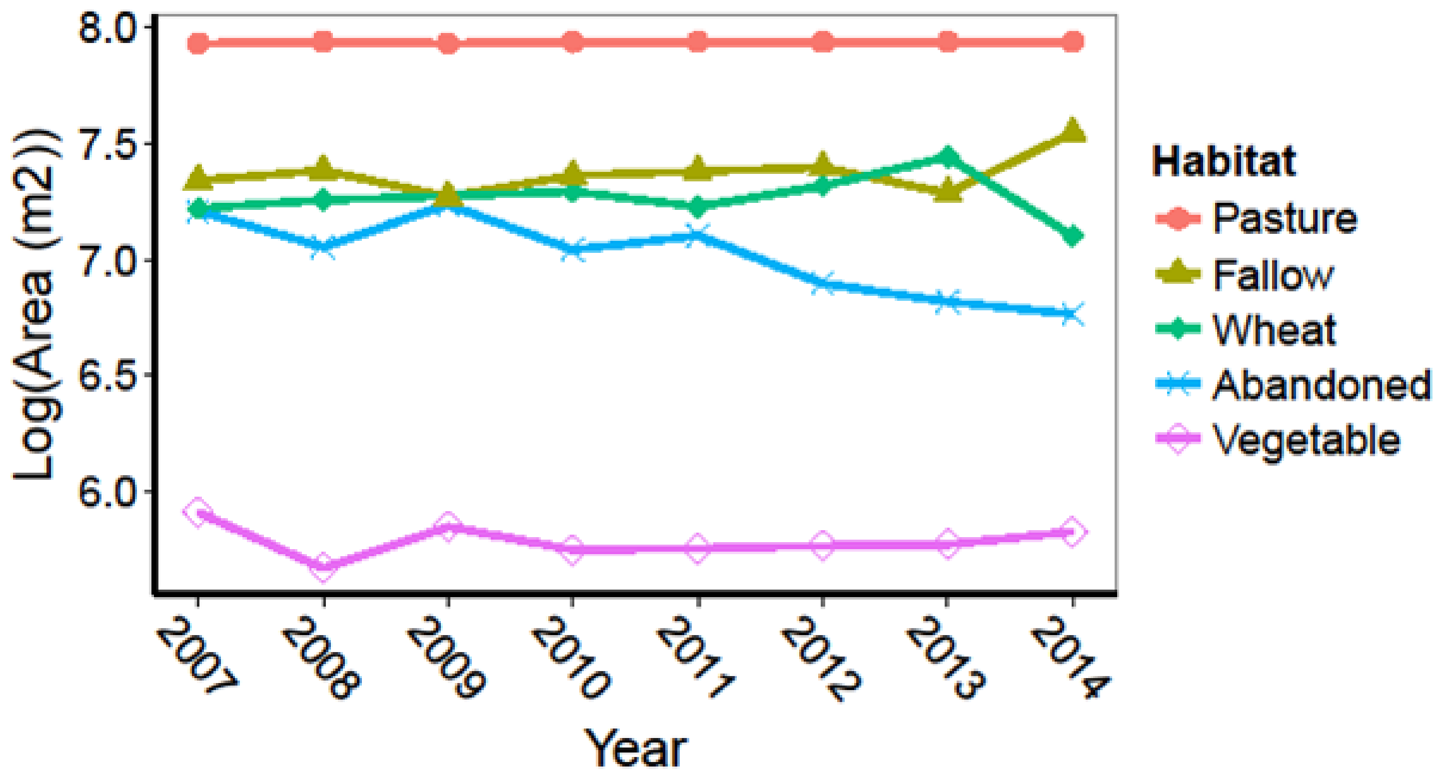

Figure 10. Area of habitat types available in each year of study. Data have been log transformed to allow all habitat types to be presented on one graph.

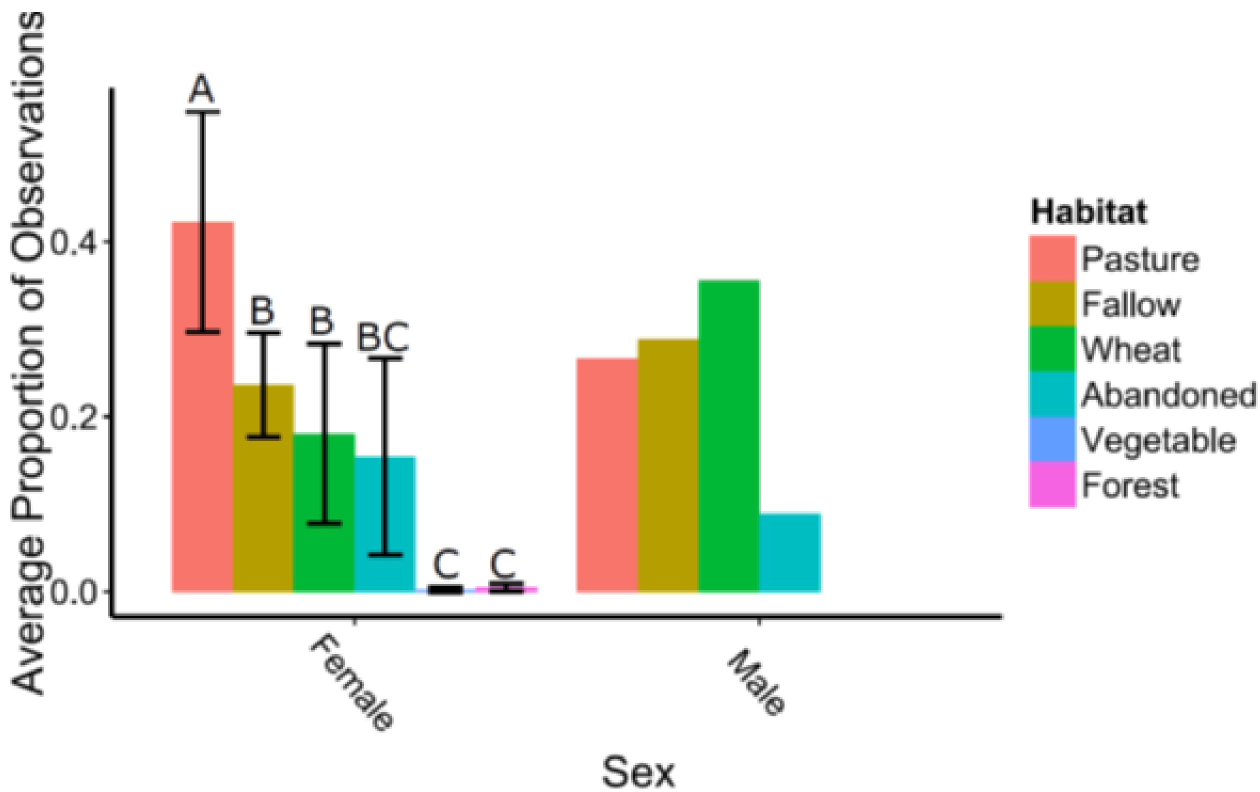

Figure 11. Proportion of observations in each habitat type for female (n=4) and male (n=1) Asian Great Bustards. Bars represent standard deviation between females observed. Bars with the same letter are not statistically different.

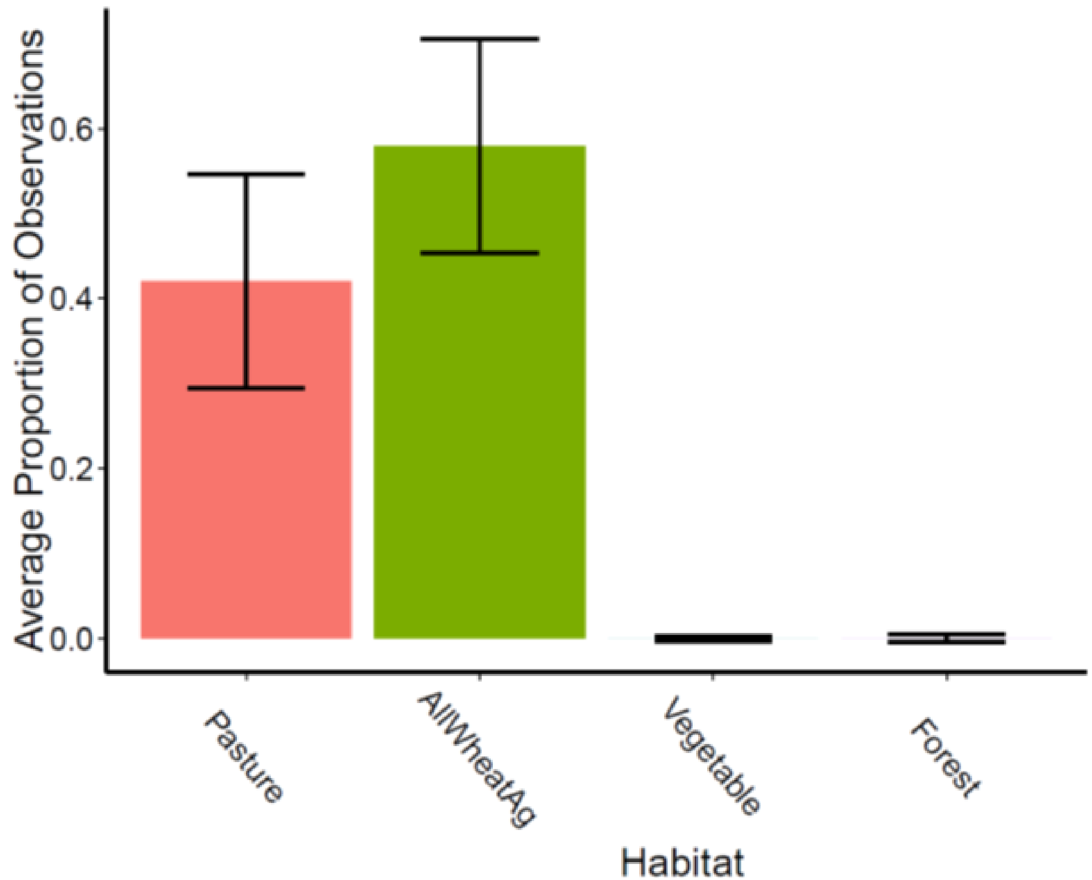

Figure 12. Proportion of observations in each habitat type for female (n=4) Asian Great Bustards. In this graph, all wheat agriculture phenologies (fallow, planted with wheat, and abandoned) have been combined into one category. Bars represent one standard deviation among females observed.

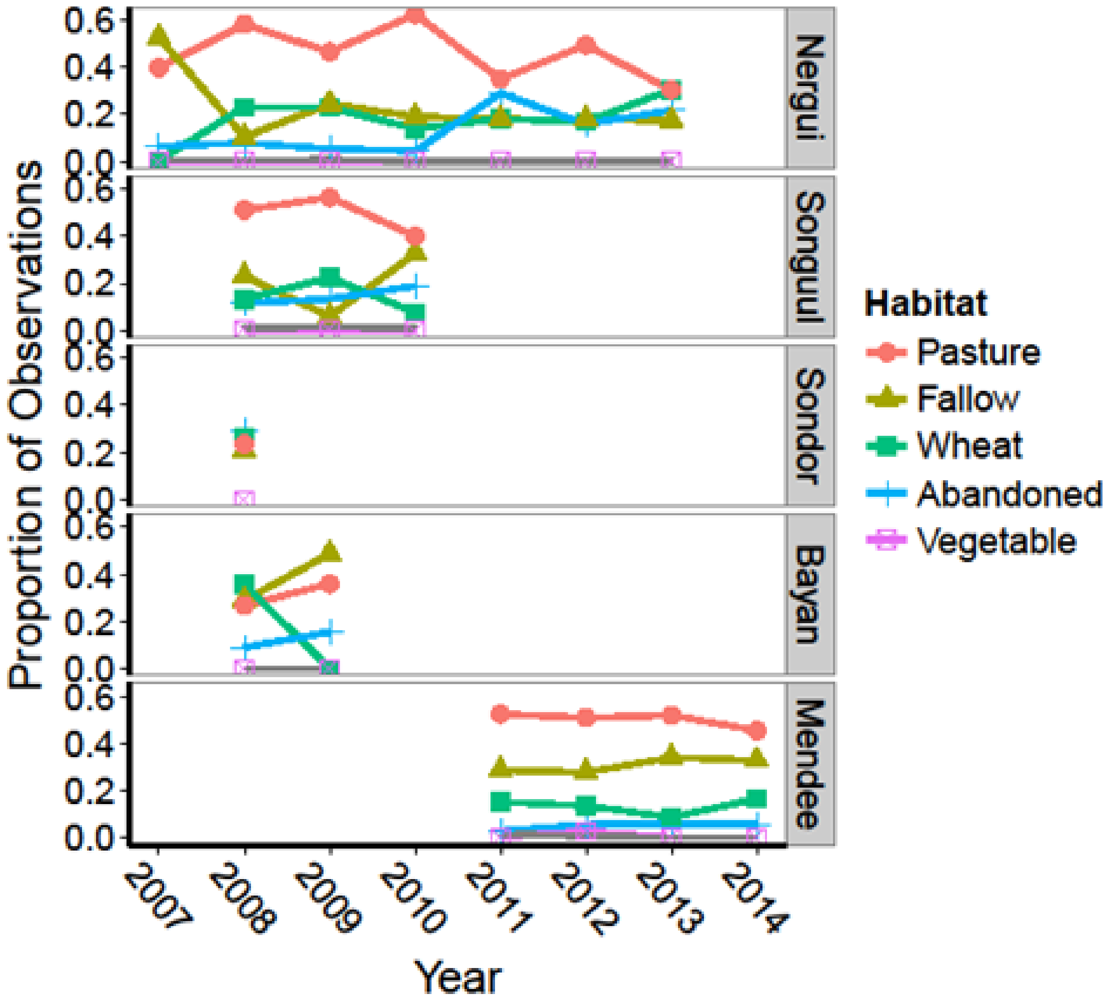

Figure 13. Proportion of observations in each habitat type in each year of study for each tagged Asian Great Bustard. Bayan was the male bird; the remainder are females.

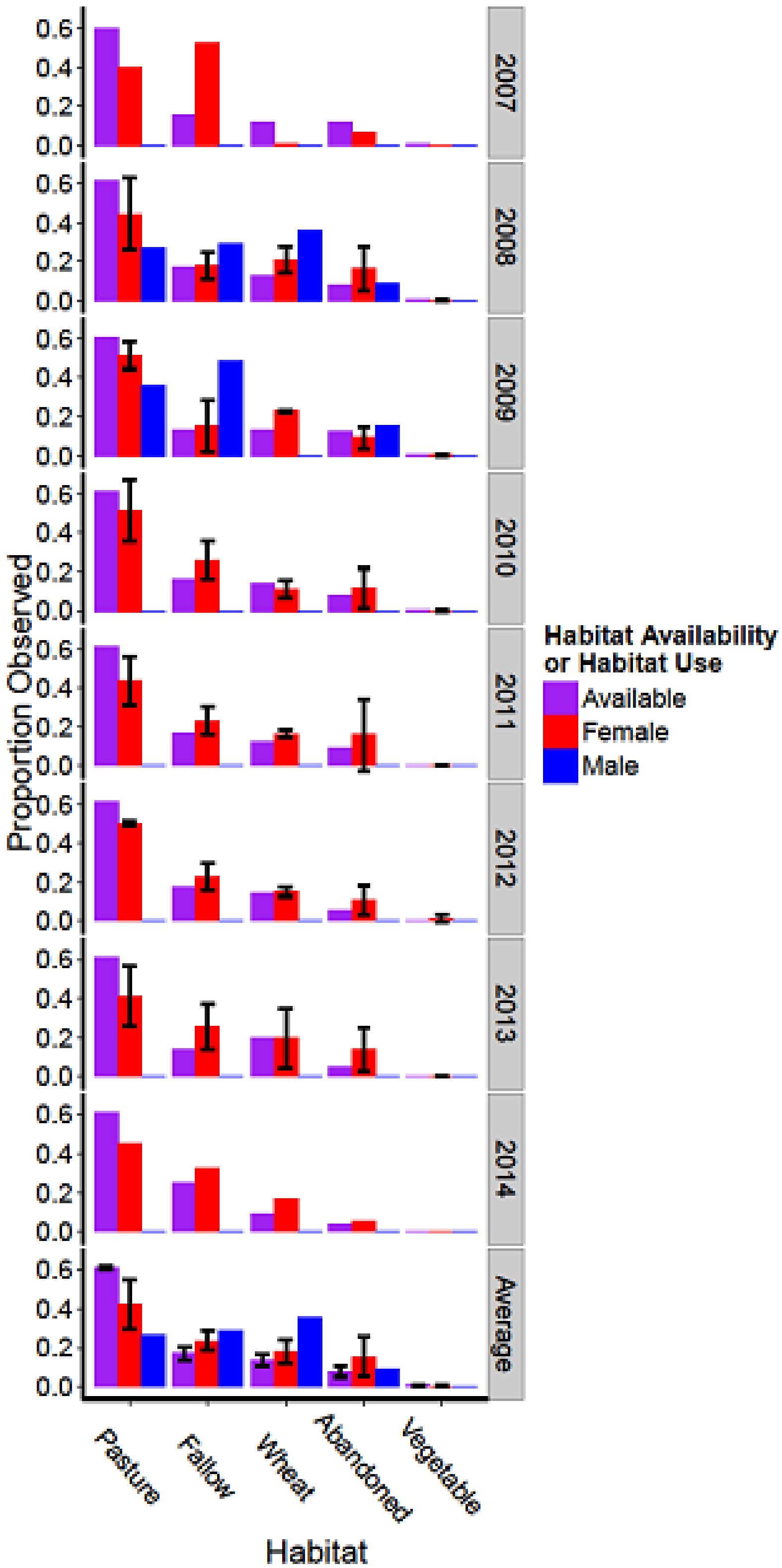

Figure 14. Comparison of proportional habitat availability and habitat use by female and male Asian Great Bustards. Bars represent one standard deviation among individual birds.

Table 6. Number and percent of GPS-satellite observations of each tagged Asian Great Bustard in each habitat type in each year of study.

Year	Name	Sex	Pasture		Fallow		Wheat		Abandoned		Vegetable		Forest		Total Locations
2007	Nergui	F	87	40%	115	53%	1	0%	14	6%	0	0%	1	0%	218
2008	Nergui	F	179	58%	32	10%	71	23%	24	8%	0	0%	1	0%	307
2009	Nergui	F	61	47%	32	24%	30	23%	7	5%	0	0%	1	1%	131
2010	Nergui	F	85	63%	26	19%	19	14%	6	4%	0	0%	0	0%	136
2011	Nergui	F	35	35%	18	18%	18	18%	29	29%	0	0%	0	0%	100
2012	Nergui	F	50	50%	18	18%	17	17%	16	16%	0	0%	0	0%	101
2013	Nergui	F	7	30%	4	17%	7	30%	5	22%	0	0%	0	0%	23
2008	Songuul	F	305	51%	137	23%	79	13%	69	12%	1	0%	5	1%	596
2009	Songuul	F	229	57%	24	6%	91	22%	54	13%	1	0%	6	1%	405
2010	Songuul	F	255	40%	208	33%	48	8%	120	19%	0	0%	5	1%	636
2008	Sondor	F	16	24%	14	21%	18	26%	20	29%	0	0%	0	0%	68
2008	Bayan	M	12	27%	13	29%	16	36%	4	9%	0	0%	0	0%	45
2009	Bayan	M	14	36%	19	49%	0	0%	6	15%	0	0%	0	0%	39
2011	Mendee	F	140	52%	76	28%	40	15%	7	3%	0	0%	4	1%	267
2012	Mendee	F	534	51%	290	28%	141	13%	56	5%	26	2%	4	0%	1051
2013	Mendee	F	329	52%	215	34%	54	9%	36	6%	0	0%	0	0%	634
2014	Mendee	F	439	45%	316	33%	158	16%	52	5%	1	0%	1	0%	967

Table 7. Ranked habitat preferences of Asian Great Bustards, obtained by carrying out compositional analysis comparing average percent of observations in each habitat type to habitat type availability. “>>” represents a significantly different use of two habitats. Because of difficulty testing the normality of data given the small sample sizes (n=5 and n=4), I performed the test with both parametric and non-parametric (randomization) methods. Habitat ranking was identical for both tests, with the exception of the last test, in which wheat fields were significantly preferred over pasture only when the data were analyzed with the non-parametric methods.

Birds Tested	Ranked Habitat	Lambda	df	Parametric *p*	Randomization *p*
All Five Bustards	CombinedWheatAgriculture>>Pasture	0.2394	1	<0.01	0.05
Four Females	CombinedWheatAgriculture>>Pasture	0.2816	1	0.02	0.12
All Five Bustards	Abandoned>Wheat>Fallow>>Pasture>>Vegetable	0.016143	4	<0.0005	0.23
Four Females	Abandoned>Fallow>Wheat>Pasture Fallow>>Pasture Randomized only: Wheat>>Pasture	0.01789	3	0.001	0.13

Table 8. Nest location and reproductive success of each female Asian Great Bustard monitored.

Year	Name	Hatched	Fledged	Habitat	Distance to Forest
2009	Nergui	Yes	No	Wheat	267 m
2010	Nergui	Yes	No	Fallow	267 m
2010	Songuul	No	No	Fallow	66 m
2010	Songuul	Yes	No	Pasture	29 m
2013	Mendee	Yes	No	Pasture	14 m
2013	Mendee	No	No	Pasture	26 m
2014	Mendee	No	No	Pasture	54 m

CHAPTER 5

CONCLUSION

The overarching goal of my research has been to increase our understanding of Asian Great Bustards (*Otis tarda dybowskii*), whose populations are greatly threatened by the recent and rapid environmental and economic changes occurring across their annual range. My studies have revealed unique adaptations of the Asian Great Bustard to the harsh Inner Asian environment, which heightens the urgency for immediate protection of these populations.

Unique traits of the Asian Great Bustard

Asian Great Bustards differ from the European subspecies in their coloration and specialized plumage used for breeding displays (Isakov 1974, Collar 1996). The breeding populations of these two subspecies are geographically isolated (Gao et al. 2008), and they lack migratory connectivity (sensu Marra et al. 2006). My research has illuminated some aspects of Asian Great Bustard ecology that further differentiate it from the European subspecies, specifically, migratory behavior and habitat use patterns.

The long-distance migration performed by Asian Great Bustards is unparalleled in the species. In contrast to the movements of central European populations of Great Bustards (Hummel 1985, Block 1996, Streich et al. 2006), the migration of the Asian Great Bustards I monitored is regular – performed each winter without regard to the severity of the winter, and with established, repeated wintering grounds. The distance of this migration is also twice as long as that of those eastern European Great Bustard populations that do perform regular migrations, and the duration approximately eight times as long (Oparina et al. 2001, Watzke 2007). Great Bustards are among the heaviest flying birds (Collar 1996, Bird 1999, Dunning Jr. 2008), and long-distance migration of the Asian Great Bustard represents a major energetic and physiological challenge that we are only beginning to understand.

The variation in migratory strategies of Asian and European Great Bustards suggests that their genetic differentiation may be substantial. Adaptation to the Mongolian climate and their distinctive migratory pattern require accommodation of a shorter breeding season. In northern

Mongolia, the beginning of the frost-free period is typically 1-11 June and lasts 90-105 days, but frosts are also possible during July and August (Lydolph 1977). The comparable period in more westerly populations is much longer (150-165 days in Saratov; 180-200 days in Berlin; 200-250 in Spain) (Linés Escardó 1970, Lydolph 1977, Schüepp and Schirmer 1977). Thus populations of Great Bustard in Mongolia begin breeding later, and chicks must develop in a shorter period of time. Additionally, as the two subspecies lack any migratory connectivity, differing selection pressures upon these two subspecies during migration, on the breeding grounds, and on the wintering grounds likely act to augment genetic differentiation. Indeed, preliminary results of genetic studies in which I collaborate indicate no shared haplotypes of the cytochrome *b* gene between Asian and European Great Bustards.

I also document a tolerance for forest edge habitat among Asian Great Bustards. European Great Bustards typically require open vistas (Johnsgard 1991, Nagy 2009), though they are occasionally described as tolerant of light tree cover (Lane et al. 1999, Palacín et al. 2012, Rocha et al. 2013). In contrast, Asian Great Bustards I monitored regularly used forest edge habitat. The transition between taiga and steppe at my research site is abrupt, with dense larch (*Larix sibirica*) forest adjacent to open meadow steppe (Hilbig 1995). Further, these Asian Great Bustards must cross substantial tracts of taiga to reach their breeding grounds each year – distances longer than the migratory journeys of most European Great Bustards.

Should Asian Great Bustard populations be lost, it may be difficult to translocate individuals from western populations. The European subspecies may lack adaptations to the Mongolian climate and to the demands of long-distance migration. Specifically, bustards from more westerly populations may not exhibit the morphological (Calmaestra and Moreno 2000, O'Hara et al. 2006, Pravosudov et al. 2007, Bowlin and Wikelski 2008, Sol et al. 2010, Baldwin et al. 2010), ontological (Meiri and Yom-Tov 2004), or neurological (Cristol et al. 2003, Mettke-Hofmann and Greenberg 2005, LaDage et al. 2011) adaptations required to successfully complete a migration of the distance and duration observed in east Asia. There may also be failure to orient correctly, migrate a sufficient distance, or to successfully time migration and reproduction in the more severe Mongolian climate due to either innate, endogenous factors or lack of appropriate parental instruction (Berthold and Querner 1981, Gwinner 1996, Hedenström 2008). Shifts in these traits would need to occur rapidly for presumably small populations of introduced birds to succeed.

Conservation outlook and recommendations

Remnant populations of the Asian Great Bustard are small and increasingly isolated from one another. Genetic studies in which I collaborate have found low genetic diversity within these populations, and conservation action should be pursued before further genetic diversity is lost. The Great Bustard is a lekking species that displays strong conspecific attraction (Alonso et al. 2004). As leks disappear, the distance between remnant leks increases, which decreases the likelihood of dispersal events and thus gene flow (Smith and Peacock 1990). The likelihood of recolonization of extinct leks also diminishes (Lane et al. 2001). Conservation work should prioritize ensuring conditions for survival of the species across its broad annual range. Successful conservation planning will require collaboration with the agricultural community and consideration of the effects of climate change.

To conserve this distinct subspecies, it is clear that conservation must be pursued at the landscape scale (Otte et al. 2007, Boyd et al. 2008). The Asian Great Bustards I monitored spent one-third of the year at breeding grounds, one-third of the year on non-repeated migratory stopovers, and one-third roaming nomadically across large wintering ranges. International cooperation is needed to ensure adequate habitat and to reduce adult mortality across the annual range. My proposal to increase protections for this species under the Convention on the Conservation of Migratory Species of Wild Animals (Appendix A) was accepted by the Eleventh Meeting of the Conference of Parties. This listing both raises the conservation profile of this species and provides a structure for international meetings and commitments to its conservation.

Though Asian Great Bustards are tolerant of agricultural activity, including nomadic pastoralism and wheat agriculture, increases in intensity of these activities are likely to cause harm. Economic incentives for pastoralists to expand their herds (Berger et al. 2013), are likely to increase disturbance of these wary birds and result in the trampling of nests (Kollar 1996, Moreira

1999, Rocha et al. 2013). Similarly, there is pressure to increase grain production at both the individual level, for personal profit, and at the national level, in the interests of food security during this period of uncertain weather and fluctuating international prices. My study found that Asian Great Bustards are tolerant of reclamation of abandoned farmland. However, the introduction of pesticides to increase crop yields would decrease the insect food base upon which Great Bustards and their fast-growing chicks rely on during the summer period (Ryabov and Ivanova 1971, Tian et al. 2004, Martín et al. 2007, Alonso et al. 2009, Bravo et al. 2013). Conservation planners should look to successful agri-environmental schemes in Europe (e.g., Pinto et al. 2005, Lóránt et al. 2013) to develop solutions that can accommodate the needs of both farmers and Great Bustards.

Finally, the climate in the range of the Asian Great Bustard is changing more swiftly than in other areas of the globe (Batima et al. 2005, Dagvadorj et al. 2009, Wang et al. 2009). My research provides some hope that the flexibility Asian Great Bustards display in their migratory behavior will allow them to adapt to changing environmental conditions. While it seems likely that desertification will increase migratory barriers, my research suggests that Great Bustards are sometimes able to delay flights until adequate conditions (whether wind support or body fat stores) are available. As temperatures warm, permafrost recedes, and patches open in the taiga, the Asian Great Bustards' willingness to traverse tree-covered territory may mean that the subspecies is able to exploit newly available habitat north of their current range, though survival of such populations would depend on reduction of hunting pressure (Ponomareva 1986, Goroshko 1999, Zabelin and Popov 2002). At the same time, the increased occurrence and persistence of late snowfall may further depress already dismal reproductive rates.

At first sight, the Asian steppe appears to be a boundless and eternal expanse, but its scale belies its fragility. Currently this ecosystem is experiencing unprecedented change as the region integrates into the globalized market economy. As one of the least protected ecosystems in the world, its future is in the hands of the herders, farmers, miners, entrepreneurs, and politicians of the region. My goal has been to understand the ecology and conservation status of the Asian Great Bustard as a charismatic symbol of this under-valued ecosystem. My hope is that my work will inspire appreciation and focus conservation action as the future of this ecosystem is shaped.

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APPENDIX A

PROPOSAL FOR THE INCLUSION OF

THE GLOBAL POPULATION OF THE GREAT BUSTARD (OTIS TARDA)

IN CMS APPENDIX I

CMS

CONVENTION ON MIGRATORY SPECIES

Distribution: General

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Quito, Ecuador, 4-9 November 2014
Agenda Item 24.1.1

PROPOSAL FOR THE INCLUSION OF THE GLOBAL POPULATION OF THE GREAT BUSTARD (*Otis tarda*) IN CMS APPENDIX I

Summary

The Government of Mongolia has submitted a proposal for the inclusion of the global population of the Great Bustard (*Otis tarda)* on CMS Appendix I for the consideration of the 11th Meeting of the Conference of the Parties (COP11), 4-9 November 2014, Quito, Ecuador.

The proposal is reproduced under this cover for a decision on its approval or rejection by the Conference of the Parties.

The Government of Mongolia has made some amendments to the original proposal and has subsequently submitted the revised version enclosed.

PROPOSAL FOR INCLUSION OF SPECIES ON THE APPENDICES OF THE CONVENTION ON THE CONSERVATION OF MIGRATORY SPECIES OF WILD ANIMALS

A. PROPOSAL: To list the global population of Great Bustard, *Otis tarda,* on Appendix I

B. PROPONENT: Government of Mongolia

C. SUPPORTING STATEMENT

1. Taxon

1.1	**Classis**:	Aves
1.2	**Ordo**:	Gruiformes
1.3	**Familia**:	Otididae
1.4	**Species**:	*Otis tarda*, including both subspecies, *O.t. tarda* and *O.t. dybowskii*
1.5	**Common name(s)**:	Great Bustard, Abetarda-comum, Avutarda, Grande Outarde, Großtrappe, Túzok,Дрохва,Дуадақ, ХонинТоодог, Дрофа, 大鸨

2. Biological data

2.1 Distribution

2.1.1 Current distribution

The Great Bustard breeds at discrete, traditional display sites (leks) across Eurasia from Portugal to Manchuria (Figure 1; Butchart & Symes 2014). The northern limits of this breeding range currently include the UK, Germany and northern Kazakhstan. The current southern limit of the Great Bustard's breeding range is described by northern Morocco, Turkey, and Nei Mongol in the People's Republic of China. This breeding distribution is characterized by a high degree of fragmentation, particularly outside of Iberia and the southwestern Russian Federation.

Irruptive movements bring Great Bustards in central Europe into countries of southern Europe. Populations in Turkey and eastward through Eurasia make regular migrations to distinct wintering grounds as far south as the Syrian Arab Republic, and Anhui Province of China.

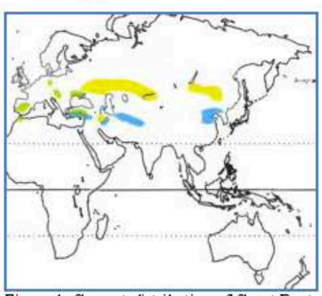

Figure 1. Current distribution of Great Bustard. Green represents habitat used year-round by some portion of the population; yellow represents breeding grounds; blue represents wintering grounds. Breeding ranges described in Kazakhstan, Mongolia, the southeastern Russian Federation and China would be more accurately represented by a number of dots, reflecting small, fragmented populations. Source: Collar (1996).

2.1.2 Historic distribution

Whereas the current distribution of Great Bustards is characterized in most portions of its range by small, disjunct populations, this species was once found more continuously across the steppe and desert-steppe belt of Eurasia, as well as North Africa and throughout cereal agriculture in western Europe. Breeding populations of Great Bustards were extirpated from Algeria, the Balkans, Bulgaria, Czech Republic, France, Poland, Romania, the Syrian Arab Republic, Tajikistan, Tunisia, and the UK (where they were reintroduced in 2004), in the 19th and 20th centuries. The number of distinct breeding populations (leks) as well as the number of individuals within remaining leks has decreased in areas of central and eastern Europe, the Middle East (Turkey and Iran), Kazakhstan and east Asia (the southeastern Russian Federation, Mongolia China).

As a result of these declines in breeding populations, Great Bustards now only rarely visit countries of the Middle East, Caucasus and Central Asia where they once regularly overwintered.

Subspecies: The nominate subspecies *Otis tarda tarda* is found from Portugal through Xinjiang, China. *O. t. dybowskii* inhabits areas east of the Altai Mountain range, in the southeastern Russian Federation, Mongolia and eastern China.

2.2 Population

The global population of the Great Bustard is estimated between 44,000 and 57,000 individuals (Alonso and Palacín 2010). The majority (57-70%) of this population is found in the Iberian Peninsula, with the second largest population center (15-25%) located in the southwestern Russian Federation. These populations are relatively stable.

Populations in central Europe representing 3-4% of the world's Great Bustards, which have been listed under Appendix I of CMS via the Memorandum of Understanding on the Middle-European Population of Great Bustard, are increasing.

However, across the greater part of this species' distribution, populations are declining. Over the past fifty years, rapid declines have occurred in the eastern half of the species range, where Great Bustards have been completely eliminated from many regions.

There is particular concern for the eastern subspecies of Great Bustard (*O. t. dybowskii*), of which only 1,200-2,000 individuals are estimated to remain in the southeastern Russian Federation, Mongolia, and eastern China (Chan and Goroshko 1998, Tseveenmyadag 2001, Alonso and Palacín 2010). These remnant populations are declining, isolated, and suffer from a lack of genetic diversity (Tian et al. 2006). Increasing threats to these populations are observed as infrastructure is developed and human settlement increases in these regions of Asia.

2.3 Habitat

Great Bustards are historically a species of open grasslands, breeding in steppe and desert-steppe zones of Eurasia as well as portions of northern Africa. The species expanded into Western Europe as forests were cleared for agriculture (Isakov 1974). Today, agricultural fields are the only available breeding habitat for Great Bustards in some areas. Active, fallow, and abandoned cereal fields are used by the species, where they feed primarily on insects and non-cereal vegetation(Lane et al. 1999, Bravo et al. 2013). The eastern subspecies is notable for its use of forest edges and small forest clearings as well as pastured grassland and cereal agricultural mosaics (Goroshko 1999, Kessler in litt.).

Wintering habitat is similar to breeding habitat. Great Bustards in agricultural fields feed on cereal stubble or alfalfa at this time of year(Lane et al. 2001).

2.4 Migrations and international movements

Great Bustards display a variety of migratory patterns across their broad geographic range, with length and duration of migration generally increasing longitudinally from west to east. This migratory behaviour and other patterns of movement (e.g. dispersal of young birds) frequently involve the crossing of one or more international borders.

Iberian populations are partially migratory, exhibiting an assortment of short seasonal movements of 10-200 km distance (Alonso et al. 2000, 2001). There was likely once regular genetic exchange between populations in Spain, Portugal and Morocco (Broderick et al. 2003), but dispersal especially to Morocco has diminished as populations on both sides of the Strait of Gibraltar have reduced (Alonso et al. 2009a).

Populations in central Europe tend towards sedentary behaviour, but facultative migrations of up to 650 km have been recorded in response to severe winter weather, bringing these birds to States in southern Europe (Block 1996, Streich et al. 2006). Within central Europe, non-migratory movements regularly result in these birds crossing international borders.

Through satellite tracking, it has been determined that female Great Bustards breeding in the south west of the Russian Federation regularly migrate 1,100 km over the course of one week to overwinter in Ukraine (Oparina et al. 2001). During the breeding season, there is likely exchange between these breeding populations and those in western Kazakhstan.

Historically, Great Bustards also migrated from the south west of the Russian Federation, and possibly western Kazakhstan, along the western shore of the Caspian to overwinter in significant numbers in Azerbaijan and Iran. Now such movements are rare (Patrikeev 2004, Rabiee and Moghaddas 2008).Though Syrian breeding populations have likely been extirpated, Great Bustards breeding or wintering in Iran and Turkey probably move into Iraq and the Syrian Arab Republic (Tareh 2000).

Historically, Great Bustards in Kazakhstan and Tajikistan migrated southward into Uzbekistan, Turkmenistan, Afghanistan and Pakistan to overwinter (Bostanzhoglo 1911, Gubin 2010). They are now rarely sighted on these wintering grounds, due to severe declines in the Great Bustard population of Kazakhstan and its extirpation in Tajikistan (Meklenburtsev et al. 1990). Today, Great Bustards wintering in south Kazakhstan irruptively migrate into Uzbekistan during harsh winter conditions (Kreitsberg-Mukhina 2003).

Results of satellite telemetry have revealed that females of the Asian subspecies of Great Bustard (*O. t. dybowskii*) breeding in north-central Mongolia take two months to migrate 2000 km into Shaanxi Province of China, making use of multiple stopovers (Kessler et al. 2013). These females move nomadically across a broad wintering range. Great Bustards in the south east of the Russian Federation probably make similar migrations through Mongolia into China.

Many Great Bustard leks in the south east of the Russian Federation and northern Mongolia are located close to the international border. These birds most likely intermittently cross the border for forage or to find desired habitat. It is probable that dispersal events once frequently occurred across this border.

It is worth noting that differences in migratory behaviour across the wide distribution of the Great Bustard appear to be distinct features of local populations, representing adaptations to local climate and geography. Priority should be placed on maintaining local populations of Great Bustards, as programmes involving the translocation of birds may face difficulty in this regard.

3. Threat data

3.1 Direct threats

3.1.1 Collision with overhead cabling

As large birds with low manoeuverability in flight, Great Bustards are highly vulnerable to collision with overhead cabling (Janss and Ferrer 2000, Raab et al. 2010). Mortalities due to collisions are reported across the species' annual range, and are expected to increase in Asia as infrastructure and industry develop. In Central Europe, international cooperation under the auspices of the Memorandum of Understanding on Middle-European Populations has resulted in the marking and burying of cables that affect neighbouring populations.

3.1.2 Hunting

Great Bustards are almost universally protected from hunting across their distribution. However, over the past fifty years, uncontrolled, illegal hunting has been a major cause of decline and even extermination of local populations of this slow-reproducing species in the central and eastern portions of its range (Chan and Goroshko 1998, Heunks et al. 2001). Poaching on both breeding and wintering grounds represents a serious threat to the survival of Great Bustard populations breeding in Turkey, Kazakhstan, the south east Russian Federation and Mongolia. The development of a more extensive paved road network in rural Asia has facilitated the travel of urban hunters to rural areas.

On migratory and wintering areas in China, Great Bustards suffer from the indiscriminate poisoning of wild birds for supply of meat to "wild foods" restaurants (Shi 2008; Chan & Goroshko 1998, Kessler in litt.). Great Bustards breeding in the south east of the Russian Federation, Mongolia and northern China use this migratory pathway.

3.1.3 Destruction of eggs and chicks

Great Bustards are ground-nesting birds with a naturally low reproductive rate. In Spain, a ten-year study found an average of 0.15 chicks produced per breeding female per year (Morales et al. 2002). Nests in natural grassland suffer from predation by corvids and canines, whose abundance may be artificially elevated around human population points. In addition, wildfires, both natural and anthropogenic, destroy nests in Asian steppe habitat. In areas used as pasture, livestock sometimes trample Great Bustard nests.

Great Bustard clutches in agricultural fields are often destroyed by agricultural machinery. In Spain, pre-hatching mortality was found to be 50% and post-hatching mortality 57%, due largely to being crushed by machinery (Ena et al. 1987). Nests that are not directly crushed may be predated by corvids which observe the flushed female. The provision of incentives to farmers to accommodate Great Bustard nests during key periods is carried out in some areas of Europe (Lóránt et al. 2013).

3.1.4 Indirect poisoning

Accidental poisoning of Great Bustards by agricultural chemicals and rodenticides is occasionally reported throughout the range of the species (e.g., Puzanskii 2000, Oparin et al. 2013).

3.2 Habitat destruction

Great Bustards require large annual territories used at low levels of development. Habitat destruction, fragmentation, and agricultural intensification have been major factors in declines of western populations of Great Bustard, and are likely to become greater factors in eastern populations as well.

3.2.1 Declining quality of breeding habitat

Timing of use of agricultural machinery, and the intensification of agricultural production are major habitat-quality threats on breeding grounds, as described in "3.1.3 – Destruction of eggs and chicks" and "3.3.1 – Agricultural chemical use." For bustards inhabiting natural grasslands, overgrazing decreases quality of forage and increases the risk of the trampling of nests.

Great Bustards are a lekking species, which perform breeding displays and nest at traditional lek sites. Due to strong philopatry (Alonso and Alonso 1992, Alonso et al. 2000), males may continue to display and females to nest at a lek site despite conversion to inappropriate habitat, with resultant high mortality and/or low breeding success that may drive the local population to extinction.

3.2.2 Declining quality of migratory stopovers and wintering areas

Eastern European and Asian populations of Great Bustard, which perform long-distance movements, require large areas of open grassland or agricultural land for foraging during migration and wintering. Increasing human population density and activity decrease the quality of habitat through disturbance. Installation of overhead cabling creates risk of fatal collisions.

3.2.3 Disturbance

Great Bustards are exceptionally wary and sensitive to human disturbance, exhibiting fleeing distances from 500 to 1,500 metres (Gewalt 1959). This trait is exaggerated in areas where they are persecuted by humans. Unsuitable levels of even benign human activity can cause Great Bustards to abandon otherwise suitable habitat.

3.3 Indirect threats

3.3.1 Agricultural chemical use

The use of pesticides and herbicides on agricultural fields where Great Bustards nest reduces the food base necessary for growth of Great Bustard chicks (Bravo et al. 2013). Male chicks are particularly vulnerable to limited food supply, as they have higher growth rates due to the species' high degree of sexual dimorphism (Martín et al. 2007).

Rates of chemical application are likely to increase in Eastern Europe and Asia. Yet, Great Bustard chicks in these areas are under greater pressure for rapid growth, as the more severe climate in these areas requires that nesting begin later in spring, and also demands that chicks be prepared for long-distance migration in the fall, including the crossing of international borders (Kessler et al. 2013).

3.3.2 Loss of genetic diversity

Increasing isolation of remnant Great Bustard leks, especially in Morocco and the Asian portion of the species' distribution, has a negative impact on genetic diversity (Tian et al. 2006, Alonso et al. 2009a). There is concern about loss of unique genetic characteristics of the Asian subspecies, which numbers less than 2,000 individuals (Alonso and Palacín 2010).

3.3.3 Climate change

As large, heavy birds, male Great Bustards are sensitive to high temperatures (Alonso et al. 2009b). Climate simulations suggest that much of the Great Bustard's current range in Europe will become unsuitable in the late 21st century. Huntley et al. (2007) find that suitable habitat will shift out of Western Europe into areas of Eastern Europe and Sweden which the species does not currently inhabit. Osborne et al. (2008) find that suitable habitat will persist in northwest Spain and Turkey, but additionally shift into France, Poland, and the Baltic states, where the Great Bustard is not currently found. It is uncertain how this highly philopatric species will adjust to changes in climate.

3.4 Threats connected especially with migrations and movements

Partial migrations performed in Western Europe, facultative irruptions in Central Europe, and regular migrations performed from Turkey eastward all expose Great Bustards to threats over a large spatial scale, including collision with overhead cabling, hunting, poisoning and habitat degradation (Yan 1982, Chan and Goroshko 1998, Oparin et al. 2003, Andryushchenko and Popenko 2012). In many regions, non-migratory patterns of movement also result in the crossing of international borders, exposing these birds to different conditions and threats.

The prolonged migration performed by the Asian subspecies, which involves use of multiple stopovers, crossing of international borders, and nomadic behaviour on wintering grounds, puts its entire population at particular risk. In a tagged cohort of female Asian Great Bustards, all observed mortalities have occurred on the migration pathway and wintering grounds (Kessler, unpublished data). Further, climate change is expanding the extent of the Gobi Desert (Wang et al. 2008), which is a obstacle for the migration of these Great Bustards.

In both facultative and regular long-distance migrating populations of Great Bustard, there appears to be a tendency for females to migrate more often or further than males. Since Great

Bustards are a lekking species in which females are solely responsible for incubation and rearing of chicks, increased mortality of females on the migration pathway has the potential to have a great impact on population growth.

High levels of mortality were previously encountered during irruptive migration events in Central Europe. With the listing of these middle-European populations on Appendix I, a system of communication was developed between Range States hosting breeding populations and Range States which periodically receive irruptive migrants. This allows these southern states to better ensure appropriate conditions for the bustards' survival.

Listing of the entire population of Great Bustard under Appendix I could promote growth in currently stable populations in the Iberian Peninsula, while slowing alarming declines in populations outside of Europe. Raising the international conservation profile of this species also has potential to affect conservation action in Range States which are non-signatories. Improvement in migratory breeding populations has the potential to restore wintering populations that have disappeared from the Middle East, Caucasus and Central Asian countries over the past century.

3.5 National and international utilization

In the past, international trade in Great Bustard feathers resulted in the listing of this species on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). This trade has largely been halted.

As described above in "3.1.2 – Hunting," Great Bustards are pursued particularly in Eastern Europe, the Middle East, and Asia. Reasons for hunting include sport, meat for personal use or trade, and curiosity about this rare bird as it is sighted on irregular stopovers. An international component to this persecution exists in the form of sport hunters arriving to Asian Range States from Western Europe and the Arabian Peninsula to pursue this species.

4. Protection status and needs

4.1 National protection status

The Great Bustard is red-listed across most of its range, at levels from Vulnerable to Extinct.

4.2 International protection status

The Great Bustard is considered as Vulnerable in the IUCN Red List of Threatened Species. The IUCN Bustard Specialist Group unanimously endorses this proposal for listing global populations of Great Bustard on CMS Appendix I.

4.2.1 Coherence with CITES

The Great Bustard is listed on Appendix II of CITES. International trade is controlled across the species' range. This listing has been successful in largely halting international trade in the species' feathers, which were once used for fly fishing.

Factors gravely threatening populations of Great Bustard, which are not related to international trade, are detailed above in Section 3. These include collisions with overhead cabling, hunting and destruction of eggs, chicks, and habitat degradation and loss. Listing of the entire population of Great Bustard under Appendix I would be an appropriate mechanism to coordinate knowledge-sharing and international efforts to reduce these threats.

4.2.2 Coherence with the Birds Directive

The Great Bustard is listed on Annex I of the European Union's Birds Directive. The Directive has supported the designation of protected areas, including 141 Special Protection Areas that hold the Great Bustard as a designation feature. The Directive also protects Great Bustards through a ban on hunting. LIFE projects providing €10 million over the last decade have focused on conservation work for the species.

Listing the global population of Great Bustards on Appendix I of CMS is consistent with the EU Birds Directive. Within Europe, this listing will further facilitate protection and restoration of habitat and help to prevent, remove or minimize the adverse effects of activities or obstacles that seriously impede or prevent the migration of the species.

Importantly, this listing will also provide a mechanism for sharing of knowledge about best practices for protection of Great Bustards (e.g., methods of marking overhead cabling; the development of cooperative agreements with farmers to ensure compatibility of the agricultural schedule with Great Bustard breeding) developed via EU projects with non-EU Range States.

4.2.3 Coherence with CMS

Currently, the global population of Great Bustard is listed on Appendix II of the CMS.

Some populations of Great Bustard are protected on Appendix I through a Memorandum of Understanding. Range States are convened for formal meetings and have developed an international species action plan (Nagy 2009). Joint action includes coordinated census programmes and cooperation to eliminate threats to neighbouring populations (e.g., burying overhead cables).

Yet, the condition of populations of Great Bustard breeding in the Middle East, Central and East Asia, as well as North Africa, is considerably worse than that in middle Europe. Central Asia now holds only 300 individuals (Mityaev and Yashchenko 2006), as does Turkey (Karakaş and Akarsu 2009). Eastern Asian populations, which comprise a distinct subspecies, contain approximately 2,000 individuals (Alonso and Palacín 2010). About 100 individuals remain in Morocco (Hellmich and Idaghdour 2002). Threats to these populations are increasing with industrial and agricultural development, and expansion of the human population. As populations from portions of the range within and east of Turkey are regular, long-distance migrants, the extirpation of local breeding populations also means reductions or elimination of stopover or wintering populations in adjacent countries. Listing of the entire species of Great Bustard under Appendix I would help to coordinate protection of these populations.

The Central Asian Flyway Action Plan provides protection to migratory waterbirds across their annual ranges in Central Asia (Convention on the Conservation of Migratory Species

2005). Listing of the entire species of Great Bustard under Appendix I would provide similar protection for this dryland migrant in this region.

4.3 Additional protection needs

4.3.1 Direct protection

Collisions with cabling: Key Great Bustard movement corridors, including stretches of cabling causing mortality should be identified. Marking of overhead cabling, or ideally, burying or re-routing of cables from known sensitive areas, should be undertaken to reduce mortality (Raab et al. 2012). The potential of cabling to cause Great Bustard mortality should be explicitly considered in large-scale industrial developments in areas where populations are critically low.

Hunting: Elimination of hunting along the migration pathway is critical to the stabilization of migratory Great Bustard populations. However, adequate enforcement of hunting bans is challenging in rural areas of the Middle East, Central and Eastern Asia. Targeted public awareness campaigns should be undertaken in these areas to raise concern and reduce hunting among local people. Where illegal sport hunting by foreign citizens occurs, fines for foreign citizens should be increased. Prohibitions in sale of wild-caught game, which is also dangerous to consumers of meat from poisoned birds, should be better enforced at markets and restaurants.

Destruction of eggs and chicks: The timing of agricultural activities, and of Great Bustard nesting, varies across its broad Eurasian distribution. In breeding habitat outside of the EU, where such measures have already been implemented, research should be undertaken to assess the degree of compatibility between agricultural practices and Great Bustard breeding. EU states can play a valuable role in sharing knowledge and experience in developing appropriate subsidy schemes to provide high-quality breeding habitat.

4.3.2 Habitat protection

Protected areas: Across the Middle East, Central and eastern Asia, surveys should be undertaken to clarify lek sites. Where possible, satellite tracking would improve understanding of migratory routes. Leks, key migratory stopover sites, and wintering grounds hosting important populations of Great Bustard should be officially protected and, where necessary, backed up with enhanced anti-poaching enforcement and disturbance-reduction measures.

Subsidies for low-intensity agriculture: Agricultural intensification has played a major role in Great Bustard declines worldwide. State subsidies should provide incentives to maintain agricultural habitat in suitable condition for breeding Great Bustards. For example, where relevant, these incentives should discourage the use of agricultural chemicals that destroy the food base necessary for the growth of chicks or encourage the use of fallow periods to lessen disturbance. EU Range States with experience in such agricultural policy should share information on successful strategies to other Range States.

4.3.3 International communication

This listing will facilitate regular communication between Range States across the broad distribution of the Great Bustard. It will encourage information sharing from Range States with experience in Great Bustard conservation measures (e.g., States participating in the Memorandum of Understanding on Middle-European Populations) on best practices.

Turkey, the Russian Federation and China are non-Party Range States hosting important migratory Great Bustard populations. Communication and cooperation on conservation planning for Great Bustards should be pursued with these States, and ideally, agreements on conservation measures signed.

Severe winter weather occasionally precipitates migration of Great Bustards into countries in which they have not regularly occurred in contemporary times (e.g. southern Europe, Uzbekistan). Communication protocols between wildlife monitors should be established such that appropriate Range States are aware of potential irruptions and prepared to increase anti-poaching enforcement in appropriate areas.

4.3.3 Additional measures

Genetic diversity: When prioritizing conservation actions in regions with low genetic diversity, precautions should be taken to maintain genetic connectivity between extant Great Bustard populations. Urgent measures should be taken to improve the condition of the Asian subspecies, which suffers from low levels of genetic diversity.

Climate change: Modelling of shifts of suitable habitat in the Asian portion of the Great Bustard's range under climate change scenarios should be undertaken. Conservation planning should place special emphasis on areas likely to maintain suitability for Great Bustard habitation under climate change conditions.

5. Range States

Active Range States: Afghanistan, ALBANIA, ARMENIA, AUSTRIA, Azerbaijan, Bosnia & Herzegovina, BULGARIA, China, CROATIA, CZECH REPUBLIC, Democratic People's Republic of Korea, GEORGIA, GERMANY, GREECE, HUNGARY, IRAN, Iraq, ITALY, KAZAKHSTAN, KYRGYZSTAN, MONGOLIA, MONTENEGRO, MOROCCO, PAKISTAN, PORTUGAL, Republic of Korea, ROMANIA, Russian Federation , SERBIA, SLOVAKIA, SPAIN, SYRIA, TAJIKISTAN, THE FORMER YUGOSLAV REPUBLIC OF MACEDONIA, Turkey, Turkmenistan, UKRAINE, UZBEKISTAN

Range States with Extinction of Breeding Population: ALGERIA, Azerbaijan, BELARUS, BULGARIA, FINLAND, FRANCE, GREECE, POLAND, REPUBLIC OF MOLDOVA, ROMANIA, SWEDEN, SWITZERLAND, SYRIAN ARAB REPUBLIC, TAJIKISTAN, TUNISIA
Great Bustards appear as vagrants in some of these countries. In others, they continue to overwinter, leading to their listing also as Active Range States.

Reintroduction: UNITED KINGDOM

Vagrant: ALGERIA, BELGIUM, CYPRUS, DENMARK, EGYPT, FINLAND, FRANCE, GREECE, IRELAND, ISRAEL, Japan, LATVIA, Lebanon, LUXEMBOURG, MALTA, NETHERLANDS, SAUDI ARABIA, SWEDEN, TUNISIA
Single vagrants or small populations occasionally reach many other countries, particularly during facultative migration due to severe weather events.

(CMS Parties are capitalized.)

(Roselaar 1980, Collar 1985, 1996, Chan and Goroshko 1998, BirdLife International 2001, Ministry of Rural Development - Hungary 2013, Butchart and Symes 2014)

6. Comments from Range States

7. Additional remarks

8. References

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APPENDIX B

ENVIRONMENTAL VARIABLES USED IN MODELING CUES FOR MIGRATORY TIMING

Variable Name	Description	Calculation	Source	Original Spatial Resolution	Original Temporal Resolution
SnowDepth	Depth of snow, if present	Geographically and temporally interpolated using bilinear method	ECMWF Global Reatmospheric Reanalysis	0.75 degrees	6 hours
Temp	Air temperature 2 m above ground	Geographically and temporally interpolated using bilinear method	ECMWF Global Reatmospheric Reanalysis	0.75 degrees	6 hours
ArcticIndex	Arctic Oscillation Index; hemispheric scale weather pattern	Temporally interpolated using bilinear method	NOAA National Weather Service Climate Prediction Center	Global metric	Daily
AirPressure	Atmospheric pressure at ground level	Geographically and temporally interpolated using bilinear method	ECMWF Global Reatmospheric Reanalysis	0.75 degrees	6 hours
Precip	Total precipitation	Geographically and temporally interpolated using bilinear method	ECMWF Global Reatmospheric Reanalysis	0.75 degrees	3 hours
WindSupport	Wind vector in an individual's flight direction	Calculated from: (1) Wind U & V data components at 10 m above ground (2) bird's desired bearing to breeding or wintering site (Safi et al. 2013)	(1) ECMWF Global Reatmospheric Reanalysis (2) Derived from bird's current location and destination (Kessler et al. 2013)	(1) 0.75 degrees (2) ±18 m GPS data	(1) 3 hours (2) NA
Crosswind	Wind vector perpendicular to an individual's flight direction	Calculated from: (1) Wind U & V data components at 10 m above ground (2) bird's desired bearing to breeding or wintering site (Safi et al. 2013)	(1) ECMWF Global Reatmospheric Reanalysis (2) Derived from bird's current location and destination (Kessler et al. 2013)	(1) 0.75 degrees (2) ±18 m GPS data	(1) 3 hours (2) NA
ChangeSnowDepth	Change in snow depth 24 hours after departure	Snow depth 24 hours after departure –snow depth at time of departure	Calculated from SnowDepth		

Variable Name	Description	Calculation	Source	Original Spatial Resolution	Original Temporal Resolution
ChangeTemp	Change in air temperature 24 hours after departure	Temperature 24 hours after departure – temperature at time of departure	Calculated from Temp		
ChangeArcticIndex	Change in Arctic Oscillation Index 24 hours after departure	AOI 24 hours after departure – AOI at time of departure	Calculated from ArcticIndex		
ChangeAirPressure	Change in atmospheric pressure 24 hours after departure	Atmospheric pressure 24 hours after departure – atmospheric pressure at time of departure	Calculated from AirPressure		
ChangePrecip	Change in precipitation 24 hours after departure	Precipitation 24 hours after departure – precipitation at time of departure	Calculated from Precip		
ChangeWindSupport	Change in wind support 24 hours after departure	Wind support 24 hours after departure – wind support at time of departure	Calculated from WindSupport		
ChangeCrosswind	Change in crosswind strength 24 hours after departure	Crosswind 24 hours after departure – crosswind at time of departure	Calculated from Crosswind		
SD4DaysSnowDepth	Variability in snow depth in the four days preceding departure	Standard deviation of snow depth in the four days previous to departure	Calculated from SnowDepth		
SD4DaysTemp	Variability in temperature in the four days preceding departure	Standard deviation of temperature in the four days previous to departure	Calculated from Temp		
SD4DaysArcticIndex	Variability in AOI in the four days preceding departure	Standard deviation of AOI in the four days previous to departure	Calculated from ArcticIndex		
SD4DaysAirPressure	Variability in atmospheric pressure in the four days preceding departure	Standard deviation of atmospheric pressure in the four days previous to departure	Calculated from AirPressure		

Variable Name	Description	Calculation	Source	Original Spatial Resolution	Original Temporal Resolution
SD4DaysPrecip	Variability in precipitation in the four days preceding departure	Standard deviation of precipitation in the four days previous to departure	Calculated from Precip		
SD4DaysWindSupport	Variability in wind support in the four days preceding departure	Standard deviation of wind support in the four days previous to departure	Calculated from WindSupport		
SD4DaysCrosswind	Variability in crosswind in the four days preceding departure	Standard deviation of crosswind in the four days previous to departure	Calculated from Crosswind		

APPENDIX C

AIC VALUES OF STEPWISE MODELS ANALYZING RELATIONSHIP BETWEEN WEATHER VARIABLES AND SOUTHBOUND MIGRATORY MOVEMENTS OF ASIAN GREAT BUSTARDS

Model Components	AIC Score	ΔAIC	Comparison to min AIC
WindSupport	885.4	-	32.2
WindSupport +Temp	869.0	16.4	15.8
WindSupport +Temp +ChangeTemp	863.2	5.8	10
WindSupport +Temp +ChangeTemp +ChangeCrosswind	854.1	9.1	0.9
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth	853.2	0.9	-
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure	853.3	-0.1	0.1
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind	853.6	-0.3	0.4
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip	855.1	-1.5	1.9
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip +ChangePrecip	854.9	0.2	1.7
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip +ChangePrecip +SD4DaysPrecip	856.1	-1.2	2.9
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip +ChangePrecip +SD4DaysPrecip +ChangeSnowDepth	857.6	-1.5	4.4
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip +ChangePrecip +SD4DaysPrecip +ChangeSnowDepth +SD4DaysCrosswind	859.0	-1.4	5.8
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip +ChangePrecip +SD4DaysPrecip +ChangeSnowDepth +SD4DaysCrosswind +ChangeAirPressure	860.4	-1.4	7.2
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip +ChangePrecip +SD4DaysPrecip +ChangeSnowDepth +SD4DaysCrosswind +ChangeAirPressure +SnowDepth	862.2	-1.8	9
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip +ChangePrecip +SD4DaysPrecip +ChangeSnowDepth +SD4DaysCrosswind +ChangeAirPressure +SnowDepth +AirPressure	864.2	-2	11
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip +ChangePrecip +SD4DaysPrecip +ChangeSnowDepth +SD4DaysCrosswind +ChangeAirPressure +SnowDepth +AirPressure+SD4DaysTemp	866.1	-1.9	12.9

Model Components	AIC Score	ΔAIC	Comparison to min AIC
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip +ChangePrecip +SD4DaysPrecip +ChangeSnowDepth +SD4DaysCrosswind +ChangeAirPressure +SnowDepth +AirPressure+SD4DaysTemp+SD4DaysArcticIndex	868.1	-2	14.9
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip +ChangePrecip +SD4DaysPrecip +ChangeSnowDepth +SD4DaysCrosswind +ChangeAirPressure +SnowDepth +AirPressure+SD4DaysTemp+SD4DaysArcticIndex+ArcticIndex	870.1	-2	16.9
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip +ChangePrecip +SD4DaysPrecip +ChangeSnowDepth +SD4DaysCrosswind +ChangeAirPressure +SnowDepth +AirPressure+SD4DaysTemp+SD4DaysArcticIndex+ArcticIndex+SD4DaysWindSupport	872.1	-2	18.9
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip +ChangePrecip +SD4DaysPrecip +ChangeSnowDepth +SD4DaysCrosswind +ChangeAirPressure +SnowDepth +AirPressure+SD4DaysTemp+SD4DaysArcticIndex+ArcticIndex+SD4DaysWindSupport+ChangeWindSupport	874.1	-2	20.9
WindSupport +Temp +ChangeTemp +ChangeCrosswind +SD4DaysSnowDepth +SD4DaysAirPressure +Crosswind +Precip +ChangePrecip +SD4DaysPrecip +ChangeSnowDepth +SD4DaysCrosswind +ChangeAirPressure +SnowDepth +AirPressure+SD4DaysTemp+SD4DaysArcticIndex+ArcticIndex+SD4DaysWindSupport+ChangeWindSupport+Change ArcticIndex	876.1	-2	22.9

APPENDIX D

AIC VALUES OF STEPWISE MODELS

ANALYZING RELATIONSHIP BETWEEN WEATHER VARIABLES

AND NORTHBOUND MIGRATORY MOVEMENTS

OF ASIAN GREAT BUSTARDS

Model Components	AIC Score	ΔAIC	Comparison to min AIC
ChangeWindSupport	1114.0	-	47.2
ChangeWindSupport +Temp	1097.8	16.2	31
ChangeWindSupport +Temp +ChangeAirPressure	1072.6	25.2	5.8
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex	1068.6	4	1.8
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip	1067.2	1.4	0.4
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind	1066.8	0.4	-
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport	1066.9	-0.1	0.1
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex	1067.4	-0.5	0.6
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex +ChangeArcticIndex	1068.1	-0.7	1.3
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex +ChangeArcticIndex +SnowDepth	1068.7	-0.6	1.9
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex +ChangeArcticIndex +SnowDepth +SD4DaysPrecip	1070.1	-1.4	3.3
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex +ChangeArcticIndex +SnowDepth +SD4DaysPrecip +ChangeTemp	1071.5	-1.4	4.7
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex +ChangeArcticIndex +SnowDepth +SD4DaysPrecip +ChangeTemp +SD4DaysTemp	1073.1	-1.6	6.3
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex +ChangeArcticIndex +SnowDepth +SD4DaysPrecip +ChangeTemp +SD4DaysTemp +AirPressure	1074.7	-1.6	7.9
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex +ChangeArcticIndex +SnowDepth +SD4DaysPrecip +ChangeTemp +SD4DaysTemp +AirPressure +SD4DaysAirPressure	1076.3	-1.6	9.5
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex +ChangeArcticIndex +SnowDepth +SD4DaysPrecip +ChangeTemp +SD4DaysTemp +AirPressure +SD4DaysAirPressure+ChangeCrosswind	1077.9	-1.6	11.1

Model Components	AIC Score	ΔAIC	Comparison to min AIC
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex +ChangeArcticIndex +SnowDepth +SD4DaysPrecip +ChangeTemp +SD4DaysTemp +AirPressure +SD4DaysAirPressure+ChangeCrosswind+SD4DaysSnowDepth	1079.5	-1.6	12.7
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex +ChangeArcticIndex +SnowDepth +SD4DaysPrecip +ChangeTemp +SD4DaysTemp +AirPressure +SD4DaysAirPressure+ChangeCrosswind+SD4DaysSnowDepth+SD4DaysCrosswind	1081.3	-1.8	14.5
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex +ChangeArcticIndex +SnowDepth +SD4DaysPrecip +ChangeTemp +SD4DaysTemp +AirPressure+SD4DaysAirPressure+ChangeCrosswind+SD4DaysSnowDepth+SD4DaysCrosswind+SD4DaysWindSupport	1083.2	-1.9	16.4
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex +ChangeArcticIndex +SnowDepth +SD4DaysPrecip +ChangeTemp +SD4DaysTemp +AirPressure+SD4DaysAirPressure+ChangeCrosswind+SD4DaysSnowDepth+SD4DaysCrosswind+SD4DaysWindSupport+ ChangeSnowDepth	1085.2	-2	18.4
ChangeWindSupport +Temp +ChangeAirPressure +SD4DaysArcticIndex +ChangePrecip +Crosswind +WindSupport +ArcticIndex +ChangeArcticIndex +SnowDepth +SD4DaysPrecip +ChangeTemp +SD4DaysTemp +AirPressure+SD4DaysAirPressure+ChangeCrosswind+SD4DaysSnowDepth+SD4DaysCrosswind+SD4DaysWindSupport+ ChangeSnowDepth+Precip	1087.2	-2	20.4

APPENDIX E

APPROVAL LETTER

FROM INSTITUTE FOR ANIMAL CARE AND USE COMMITTEE

Institutional Animal Care and Use Committee (IACUC)
Arizona State University

Tempe, Arizona 85287-3503
(480) 965-4387 FAX: (480) 965-7772

Animal Protocol Review

Protocol Number:	07-924R
Protocol Title:	The Great Bustard in Kazakhstan and Mongolia: From Conservation Biology to Land-Use Planning
Principal Investigator:	Andrew Smith
Date of Action:	03/02/2007

The animal protocol review was considered by the Committee and the following decisions were made:

- ☐ The original protocol was APPROVED as presented.
- ☒ The revised protocol was APPROVED as presented.
- ☐ The protocol was APPROVED with RESTRICTIONS or CHANGES as listed below. The project can only be pursued, subject to your acceptance of these restriction or changes. If you are not agreeable, contact the IACUC Chairperson immediately.
- ☐ The Committee requests CLARIFICATIONS or CHANGES in the protocol as described below. Approval is contingent upon review and approval of the required revisions by the IACUC Chair.
- ☐ The protocol was approved, subject to the approval of a WAIVER of provisions of NIH policy as noted below. Waivers require written approval from the granting agencies.
- ☐ The protocol was DISAPPROVED for reasons outlined in the attached memorandum.
- ☐ The Committee requests you to contact ________________ to discuss this proposal.
- ☐ A copy of this correspondence has been sent to the Vice President for Research.

RESTRICTIONS, CHANGES OR WAIVER REQUIREMENT:

Approved number of Animals: 180 Great Bustard
Pain Level: II

Approval Period: 03/02/2007 – 03/01/2010

Signature: D Murphy ______________________ Date: 03/02/2007
IACUC Chair or Designee

Investigator
cc: IACUC Office, IACUC Chair, ORSPA, DACT

PI