Habitat, abundance and productivity of the Asian Houbara *Chlamydotis macqueenii* in Uzbekistan

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Contents

Abstract

For a species threatened with exploitation, before embarking on *ex situ* measures such as population reinforcement through captive breeding, it is important to explore potential *in situ* measures that could be used to mitigate species off-take by supporting breeding productivity of wild populations. Asian houbara *Chlamydotis macqueenii* is a globally threatened bird, with continuing declines across Central Asia, mainly due to unregulated hunting and trapping during migration and in winter. This research aims to improve understanding of the breeding season biology of the Asian houbara migratory populations in Central Asia to inform *in-situ* conservation of the species. Spring fieldwork during 2012–2015 involved distance sampling, nest monitoring and habitat sampling across 14,500 km^2 of the Kyzylkum Desert in Uzbekistan. Contrary to expectations, there appeared to be no negative landscape-scale association between livestock density and the abundance of male houbara, and no grazing effect on desert shrub vegetation. Habitat characteristics selected by males at the landscape scale were more likely to maximise visibility of their displays, with higher male abundance in lower shrub vegetation, on gravelly substrate and flatter terrain. The first robust estimate of local male density stratified by different habitats and an estimate of regional numbers were obtained. Houbara nesting success was unaffected by variation in shrub species composition or livestock density, but nests placed within taller vegetation experienced greater success. Satellite-tracking revealed high site-fidelity of males to their display sites and intra-seasonal fidelity of females to breeding areas. During post-breeding dispersal adult birds were found to be using completely different, more productive in terms of vegetation, areas outside their breeding season range. In conclusion I discuss potential implications of key findings for the conservation and management of the Asian houbara population in the Kyzylkum, and their potential relevance to other houbara populations and study systems, and suggest priorities for further research.

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Chapter 1 – General Introduction

Evidence-based conservation and sustainable management of exploited species

Unsustainable use, destruction of habitats and invasive species have caused rapid loss of biodiversity in the last few centuries, with over 600 vertebrates listed by IUCN as ‘extinct’ or ‘possibly extinct’ since 1500, of which the majority happened during the last 100 years (Ceballos et al. 2015). Human population growth and the rapid economic development of recent decades continue to put pressure on biodiversity at an ever-increasing rate, bringing more species to the verge of extinction (Butchart et al. 2010, Donald et al. 2013) and causing dramatic declines in formerly very abundant species (Milner-Gulland et al. 2001, Kamp et al. 2015).

Although conservation efforts have developed in parallel with the increasing human threats to biodiversity and are often successful in addressing them (Butchart et al. 2006, Hoffmann et al. 2010), the quality and effectiveness of conservation actions is often inadequate. Conservation management activities are still frequently based on anecdotal information and personal experience rather than being informed by scientific evidence (Sutherland et al. 2004). For instance, until recently the majority of European management plans were either based on expert opinion or relied heavily on traditional management practices (Pullin et al. 2004). Although conservation management based on personal expertise or tradition can often achieve the right results using simpler and more cost-effective solutions, it also may lead to wrong decisions or can prevent managers from using more appropriate practices (Sutherland et al. 2004). This circumstance indicates the need for evidence-based conservation advocated in recent years (Pullin and Knight 2003, Pullin et al. 2004, Sutherland et al. 2004).

Human beings have been exploiting wildlife since *Homo sapiens* evolved, and even in the distant past such exploitation sometimes led to species extinctions. Today; hunting and trapping for food and medicine is the second most severe worldwide threat to mammals after habitat loss and the fourth main threat to birds after agriculture, logging and invasive species (Vié et al. 2009).

To protect a species from persecution, direct conservation measures can sometimes be successful, with legal protection as the most commonly used intervention.

In birds, a range of studies reported species recoveries at local and regional scales as a result of the successful implementation of legislation, e.g. for birds of prey (Noer and Secher 1983, Donazar and Fernandez 1990, Baines et al. 2008), parrots (Cahill et al. 2006, Pain et al. 2006), farmland birds (Donald et al. 2007) and other species (Skira et al. 1986, Davis 1998). Giving a species a 'protected' status may sometimes be enough to shield it from exploitation, but more often 'on-the-ground' actions are also required to enforce the law (Vaughan et al. 2005, Granadeiro et al. 2006). Another conservation measure is the establishment of protected areas, which is regarded as one of the most successful measures implemented for the conservation of biodiversity (Naughton-Treves et al. 2005, CBD 2010, Watson et al. 2014). However, both 'on-the-ground' conservation and site protection might not always be enough, and both can be particularly difficult to implement for a widely distributed or migratory species, ranging across political boundaries (UNEP/CMS Secretariat 2014).

Currently large numbers of people in underdeveloped countries depend on wild animals, which have been traditionally and sustainably hunted for subsistence for centuries. However, more recently, growing human populations and the demand for 'bushmeat' for direct consumption or trade have greatly diminished populations of exploited animals (Milner-Gulland and Akçakaya 2001, Zapata-Rios et al. 2009, Fa et al. 2014, Doughty et al. 2015). At the same time, in developed countries, many species are hunted mostly for recreation and are managed exclusively for hunting. Game hunting often involves introductions and large-scale releases of native and non-native captive-bred species, with probably the most well-known examples among birds including Common Pheasant *Phasianus colchicus* and Red-legged Partridge *Alectoris rufa* (Sokos et al. 2008, Díaz-Fernández et al. 2012). Non-native species are likely to directly affect survival of local species through resource competition, altering habitat, spreading disease and producing accidental by-catch of native species (Dolman and Waber 2008, Bicknell et al. 2010, Díaz-Fernández et al. 2013).

When it is impossible to regulate hunting of a threatened species, another possibility is to support breeding productivity of wild populations as a way of mitigating exploitation – *in situ* ('on the ground') conservation. Another way is to complement wild populations by releasing captive-bred birds – *ex situ* conservation (CBD 2010). Prior to embarking on using the latter approach, two important questions need to be answered. First: Is there no *in-situ* conservation alternative? Captive breeding is sometimes viewed as the first or easiest choice for managers when in reality it is usually better considered a last resort in species recovery, to be used only when alternative *in situ* conservation measures have failed or, after thorough consideration, are expected to fail (Snyder et al. 1996, Dolman et al. 2015). The second important question to answer is: How confident are we that captive breeding and release will be successful? There are many cases when conservationists or managers failed to ask such questions and chose to start captive breeding and release programs, diverting efforts from *in situ* conservation and causing some attempts to fail (Cade and Temple 1995, Rabinowitz 1995, Linklater 2003). At the same time, there are many examples of successful captive breeding and release, mostly used for the restoration of near-extinct species (Jones et al. 1995, Kuehler et al. 1995, Kuehler et al. 2000, Van Heezik et al. 2005, Urbanek et al. 2010), for the re-introduction of locally extinct populations (Wiemeyer 1981, Sarrazin et al. 1996, Evans et al. 1999) or for the reinforcement of declining populations (Zwank and Wilson 1987, Page et al. 1989, Powell and Cuthbert 1993).

Ex situ management

In birds, captive breeding usually involves artificial incubation of eggs, hand-rearing and subsequent release of captive-bred birds. As artificial incubation techniques can be extremely complex and hand-rearing can be time- and labour-intensive, captive breeding programs are often very costly. Even if captive breeding itself is successful and a substantial stock of captive-bred individuals is established, to justify the investment in the program a population must survive in the wild long enough following the release to reproduce and become firmly established. An array of factors can negatively affect post-release survival of captive-bred birds, including predation, low fitness, lack of experience of living in the wild, availability of resources and habitat suitability (Martin et al. 1996, Snyder et al. 1996, Combreau and Smith 1998, Parish and Sotherton 2007, Dickens et al. 2010, Burnside et al. 2012). Additionally, there are behavioural, genetic, disease and domestication risks to captive-bred birds (Snyder et al. 1996, Muñoz-Fuentes et al. 2008, Williams and Hoffman 2009, Chargé et al. 2014), which in turn may have negative and unpredictable effects on wild individuals. Therefore, in order to avoid the diversion of resources and attention from potential alternative *in situ* conservation, a thorough evaluation of such *in situ* measures should be conducted prior to attempting captive breeding (Dolman et al. 2015).

In situ management

Breeding productivity of a species is influenced by many, often interdependent factors, such as habitat suitability, predation rates, resource availability and breeding density, which need to be thoroughly understood to increase the chances of successful *in situ* conservation. Understanding species' habitat requirements is a key to any 'on the ground' conservation, as the identification of optimal habitat and the most productive areas will allow their protection and management aimed at increasing productivity of the species. In heterogeneous environments, understanding landscape-scale variation in productivity is needed to identify areas that determine regional-scale demography (Waber et al. 2013). Individuals may occupy optimal habitats when numbers are low, but spread into poorer habitats when numbers increase, reducing mean reproductive rates through buffer effects (Brown 1969, Dolman 2012). Across habitats, avian reproductive success is most often positively related to density, suggesting that density is an appropriate indicator of habitat quality, the effects of which are not fully compensated by any density-dependent reduction in preferred habitats (Bock and Jones 2004). Habitat assessment can often be very time-consuming when field measurements are involved, especially if several habitat characteristics (e.g. vegetation height and density, plant species composition, tree size, topography, etc.) are thought to affect bird abundance and reproductive success. However, with increasing availability and accessibility of remotely sensed habitat measures, such as Globcover, NDVI, DEM or Lidar, relating species data to habitat becomes possible for many studies, even at a large scale (see below, Habitat assessment).

Bird nests are inevitably targeted by predators. If the nesting success of a species is believed to be compromised by predation it is important to identify the key predator/s and quantify the effects they are having on the prey species. Rapid technological advances and the reduction in costs of nest cameras now allow researchers to identify and quantify nest predators and to validate their interpretation of signs of nest outcome (Macdonald and Bolton 2008, Teunissen et al. 2008, Eglington et al. 2009, Sheldon et al. 2013). Once key predators are identified, predator control is often used as the most effective way of tackling the predation threat, and has been successfully used to increase breeding productivity of many bird populations (Côté and Sutherland 1997, Smith et al. 2010). However, this measure can sometimes be inappropriate, even if predation has a detrimental effect on productivity, and other measures need to be considered. Additionally, among other factors, trampling of nests by livestock (Moore 2005, Pauliny et al. 2008) and human disturbance (Gill and Sutherland 2000, Gill et al. 2001, Finney et al. 2005, Pearce-Higgins et al. 2007) may sometimes have a substantial negative effect on breeding productivity and need to be remedied.

Habitat assessment

Species-habitat models use empirical data to relate species to environmental predictors to define the direction and shape of the relationship, and are most often used to test for the effects of environmental predictors on species' distributions (Gunnarsson et al. 2006, Elith and Leathwick 2009, Oppel et al. 2012), abundance (Tozer et al. 2010, Jacobs et al. 2012) or productivity (King et al. 2009, Sheldon et al. 2013).

There are several main types of habitat modelling, most of which deal with species distribution. Expert knowledge-based species-habitat predictive models are based on suitability ranking and are used in conservation planning when data are scarce (Drew and Perera 2011, Iglecia et al. 2012). Habitat suitability models (HSM), which assess whether a habitat is considered suitable for a particular species based on suitability scores assigned to each cell of the map, can also be useful with limited data (de Baan et al. 2015). However, possibly the most widely used technique is species distribution modelling (SDM) (Elith and Leathwick 2009). As species count or presence-absence data are usually spatially limited, such models are then often used to predict species occurrence and distribution at wider scales. As the quality and accessibility of large-scale remotely sensed environmental datasets increase, it becomes possible to make such predictions for entire distribution ranges (Rushton et al. 2004).

Environmental predictors can exert direct or indirect effects on species, with three main types of influence recognised: (i) limiting factors, defined as factors controlling species' physiology (e.g. temperature, habitat, topography); (ii) natural or human-induced disturbances and (iii) resources, defined as all compounds that can be assimilated by organisms (e.g. energy and water) (Guisan and Thuiller 2005). To assess the significance of the relationship between species' occurrence or abundance and various habitat factors, such statistical techniques as generalized linear or generalized additive models are often used (Segurado and Araújo 2004). Taking this one step further, presence-absence or abundance data from sampled areas can be used to create maps of a species' predicted probability of occurrence at any pixel in the landscape and at a wider scale (Donald et al. 2012, Oppel et al. 2012). To create such maps a combination of tools is sometimes used, where environmental data are often collated and extracted using Arc GIS (and similar software), modelled in statistic software (R, S-Plus, SAS) and loaded back into GIS software to create distribution maps. Stand-alone habitat modelling packages are alternatively used, among which Maxent is probably the most popular, allowing modelling species distributions with presence-only data (Phillips et al. 2006).

Methodological issues and limitations

Model selection remains one of the main issues in modelling. In the last decade a radical shift to the use of information-theoretic approaches to modelling has been observed, gradually replacing modelling based on a null hypothesis-testing (Rushton et al. 2004), particularly after the publication of a milestone paper by Burnham and Anderson (2002). Although hypothesis testing has a very important role in the design and analysis of experiments where researchers have control over response and the predictor variables, Burnham and Anderson (2002) concluded that the value of this approach in the analysis of observational studies is less clear.

Distance sampling is widely used to estimate density and abundance, and controls for the decline in detectability of individuals more distant from the observer (Marques et al. 2007). Although it is possible to model abundance incorporating covariates by using 'density surface modelling' within DSM engine in Distance or 'dsm' R package, this approach is more complex and is still under evaluation and development (Miller et al. 2013). Thus multivariate effects of land-use, land cover and context are not explicitly modelled and must be controlled for in survey design. In contrast, multivariate species-habitat models can be used to investigate environmental and land-use effects on relative abundance and distribution, but their ability to predict abundance depends on appropriate error structures, detectability and scale of sampling unit. Binomial mixture models (BMM) are increasingly popular, as these allow the effects of habitat and landscape variables on local abundance to be modelled while accounting for imperfect detection, using spatially and temporally replicated counts in a closed population (Kery et al. 2005).

Despite numerous extremely useful practical applications of species-habitat modelling, there are a number of key limitations to consider when using or interpreting the results. Probably the most important of these is related to the frequent inability of a given study to consider all factors which might have substantial effects on species numbers, distribution or survival. In SDM analysis there are additional limitations resulting from data deficiencies, e.g. missing covariates, small or biased samples of species occurrences or lack of absence records (Barry and Elith 2006).

Conservation of the exploited Asian houbara *Chlamydotis macqueenii*

Asian houbara *Chlamydotis macqueenii* is a member of the bustard (Otididae) family, which consists of 26 species, with more than half of them listed as threatened or near threatened (BirdLife International 2015a). It is a medium-sized sandy-coloured bustard with black-tipped white crest and black neck-stripe (BirdLife International 2015b). The species' range extends from the Nile River in Egypt to the Gobi Desert in Mongolia (Collar 1980, Goriup 1997). The western populations, occupying the Arabian Peninsula and parts of Iran, are resident. Northern populations, breeding in the deserts and semi-deserts of Kazakhstan, Uzbekistan, Mongolia and China, are migratory and winter in the countries of Middle East, Pakistan and Afghanistan, with a migratory divide between eastern and western breeding populations (Judas et al. 2006, Combreau et al. 2011) (Fig.1).

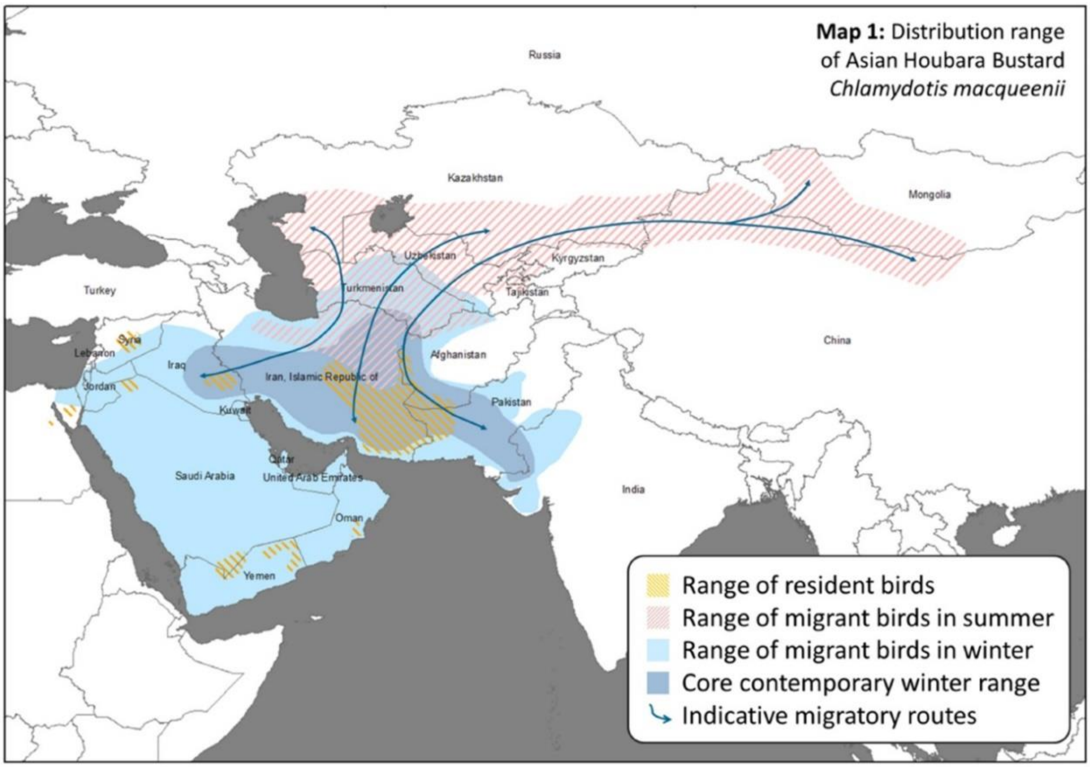

Fig.1 Distribution range and main migratory routes of Asian houbara *Chlamydotis macqueenii*. Source: (BirdLife International 2014). Map is based on BirdLife's species distribution data adapted following Riou et al. (2012) and feedback from expert contributors.

Throughout its range the Asian houbara inhabits sandy, stony and clay deserts and semi-deserts, and is very well adapted to arid conditions, typically with sparse vegetation cover and lack or complete absence of water sources (Collar 1980, Goriup 1997, Gubin 2004). Its diet is mainly comprised of invertebrates, green shoots and small reptiles, with the importance of particular types of food greatly depending on temporal and spatial availability (Tigar and Osborne 2000, Gubin 2004).

During the breeding season males hold territories where they conduct an elaborate and conspicuous display, consisting of a straight or circular run with the head placed on the back and all head and neck display feathers fully erected, and ending in a series of upward head-kicks, accompanied by a relatively quiet series of calls (Gaucher et al. 1996). The species' breeding system is described as 'lek-like' (Riou and Combreau 2014), with a more uniform distribution of male territories across the landscape than in the 'exploded-leks' described for its closest relative, the African houbara *Chlamydotis undulata* (Hingrat and Saint Jalme 2005). Females lay their eggs on the ground near male territories (Riou and Combreau 2014), and are highly cryptic during incubation. This explains the scarcity of data on houbara nesting ecology, as the location of each nest involves much time and effort. Chicks are semi-precocial and in the first days of life are fed by female, who usually takes care of them for approximately two months until they are able to fly well and become completely independent (R. Burnside unpublished). These birds are reluctant to fly, and respond to disturbance or minor threats by skulking or running away, taking wing only when flushed or under serious threat (personal observations).

Asian houbara has been recently split from African houbara (del Hoyo and Collar 2014) and is currently listed as Vulnerable by IUCN (IUCN 2015). It is included in appendices of CITES (Appendix I) and CMS (Appendix II). The IUCN threat status is justified by the near-extirpation of resident populations in the Arabian Peninsula and significant recent and continuing declines across Central Asia, mainly caused by unregulated hunting and trapping during migration and in winter (Tourenq et al. 2005, Judas et al. 2006, Riou et al. 2011, BirdLife International 2015b).

The Asian houbara has traditionally been the most prized quarry for Arab falconers and has been sustainably hunted for centuries in the Middle East. However, by the end of the last century the increased frequency and scale of hunts and their use of all-terrain vehicles, plus sophisticated navigation and communication technologies, led to the extirpation of the species from many parts its Middle Eastern range. At the same time, following the collapse of the Soviet Union in 1991, many countries in Central Asia opened their borders, allowing the exploitation of local houbara populations by Middle Eastern hunting parties. Kazakhstan, Uzbekistan and Turkmenistan are the remaining strongholds of the Asian houbara, and although it is listed as threatened in red data books of all of these countries (Kovshar 1996, Grigoryants 2010), government decrees have been issued to allow annual hunting quotas to Middle Eastern falconers (Government of the Republic of Kazakhstan 2014, Government of the Republic of Uzbekistan 2015). As ‘on the ground’ quotas are poorly enforced, how many houbara are actually hunted by each hunting party remains unknown. Considering that there are several such concessions along the major migratory routes, the overall scale of off-take in Central Asia may be substantial. Probably a more serious threat to Asian houbara populations lies in poorly regulated hunting (similarly allowed through quotas) and illegal trapping of live birds on their wintering grounds and more southerly pass-through regions, in Iran, Afghanistan and especially Pakistan. Most winter mortalities of houbara tagged on the breeding grounds in Kazakhstan and Uzbekistan are attributed to hunting or trapping (Combreau et al.

2001, R.Burnside unpublished). Although there are no published assessment of the scale of such illegal houbara off-take on wintering grounds, there are reports of annual houbara hunting quotas issued in Pakistan with hundreds and even thousands of houbara hunted (Dawn News 2014, Arab News 2015), as well as some evidence of illegal hunting and trapping for smuggling to the Middle Eastern countries (The Express Tribune 2015). Additionally, there is evidence of illegal trapping of live houbara for sale to be released elsewhere for hunting or for training falcons (BirdLife International 2015b).

Captive breeding of both African and Asian houbara has been used as a reintroduction tool for locally extinct populations and as a reinforcement of depleted populations across the Middle East and Northern Africa (Seddon et al. 1995, Saint Jalme et al. 1996, Combreau and Smith 1998, van Heezik and Ostrowski 2001, Islam et al. 2012). More recently, breeding centres have been established in Kazakhstan and Uzbekistan, following agreements between local governments and Middle Eastern falconers to use them for the mitigation of hunting off-take. With the wealth of knowledge and experience of breeding this species in captivity accumulated over several decades, such breeding centres are able to produce and maintain large stocks of birds, annually releasing hundreds or even thousands of birds into the desert. However, the demographic consequences of large-scale releases for reinforced populations are unreported, and genetic, disease and domestication risks to wild populations of any reinforced species are unknown (Snyder et al. 1996, Frankham 2008, Williams and Hoffman 2009, Dolman et al. 2015). Given such risks, the opportunities for *in situ* conservation measures should therefore first be evaluated (Dolman et al. 2015).

Deserts

Deserts cover around 17% of the world's land surface and support surprisingly rich biodiversity (Safriel 2005). They are also home to approximately 6% of the world's human population (Mortimore et al. 2009), including some of the most marginalized and poorest people in the world (Middleton et al. 2011). Historically, in terms of conservation and research, deserts have been disproportionally neglected compared to other biodiversity habitats such as tropical forests, with substantially more scientific publications in ecology in recent years focused on forest biomes (67%) compared to deserts (9%) (Durant et al. 2012).

The main characteristic of a desert is its aridity, with associated limited precipitation and extreme temperatures affecting desert soil, flora and fauna. Deserts are mostly associated with a hot climate and tropical zones, but conditions in some northern Eurasian deserts, such as the Gobi, Taklamakan and Kyzylkum, are even more extreme owing to their continental climate, as they experience both very high temperatures in summer and sub-zero temperatures in winter.

Many desert birds are well adapted to negotiate such harsh environments. To cope with high temperatures and lack of water some species have evolved to reduce their basal metabolic rate and total evaporative water loss than birds of more temperate zones (Williams and Tieleman 2005). The distribution of food is also greatly affected by inter-annual variations in habitat productivity and the short vegetation growth period in spring (following rain), which suggests large home ranges and weak inter-annual site-fidelity for desert bird species. To be able to adjust to seasonal and inter-annual variation in habitat quality and availability of resources, desert birds may also be flexible in their breeding strategy. For example, several desert lark species may not breed during drought years and produce fewer and smaller clutches per season than mesic larks (Williams and Tieleman 2005).

Pastoralism

Dryland rangelands, which include both deserts and semi-deserts, support approximately 50% of the world's livestock (Puigdefabregas 1998). Pastoralists are the major users of arid and semi-arid regions, and there is a widespread negative attitude towards grazing supported by evidence that it contributes to desertification (Lamprey 1983, Sinclair and Fryxell 1985). Additionally, high livestock densities are often blamed for having negative effects on wildlife through affecting structure and composition of desert vegetation (Sutter and Ritchison 2005, Behnke 2006, Saiz and Alados 2012) and through disturbance of breeding birds and trampling of their nests (Jensen et al. 1990, Johnson et al. 2011). Policy-induced marginalisation of nomads and the restriction of their livestock movements may often cause pastoralism to degenerate from sustainable levels into either overexploitation (MEA 2005) or degradation of dryland rangelands following prolonged rest (Olaizola 1999, Cummins 2009). But is there always a conflict between grazing and the rangeland ecosystem? A clash of opinions led to the development of non-equilibrium concepts of arid and semi-arid grazing systems (Behnke et al. 1993). In contrast to the earlier view that plants and grazing animals live in a sort of equilibrium, advocates of the non-equilibrium concept argue that their populations are governed by different "nonequilibrial" processes, suggesting instead that desert plant production is governed by highly variable rainfall and is unaffected by the density of grazing animal populations (Illius and O'Connor 1999, Sullivan and Rohde 2002).

Study system

The Asian houbara research and conservation programme was launched in 2012 in Uzbekistan by BirdLife International, University of East Anglia and the Emirates Bird Breeding Centre for Conservation, with the declared mission to demonstrate and advocate a model approach to the conservation and sustainable hunting of houbara. During the subsequent four years, detailed research into many aspects of the houbara's biology, such as breeding productivity, abundance, migration and habitat and range use, have been undertaken, focusing on both wild and captive-bred released houbara.

As part of a larger program, research for this thesis has been conducted within the study site (approx. 25,000 km^2) located in the southern part of the Kyzylkum desert within the Bukhara administrative district of Uzbekistan. The Kyzylkum desert lies within 'the Central Asian southern desert' eco-region, part of 'the Desert and xeric shrub lands biome' of 'the Palearctic (Eurasian) bio-geographic realm' (Olson 2001). This eco-region extends north into southern Kazakhstan and south and west through much of Turkmenistan. 'The Central Asian southern desert' is the richest desert complex in Eurasia, with high levels of endemism, particularly in plants, invertebrates and reptiles (Rachkovskaja and Pereladova 2012). The climate of the southern Kyzylkum desert is characterised by variably cold winters (mean monthly temperatures 0–5°C, regularly reaching -25°C), hot summers (mean monthly temperatures 27–29°C, often reaching 45°C), and annual precipitation of 125–170 mm, mostly during winter and spring. The landscape is predominantly flat or slightly undulated, bounded by low mountain ranges to the north and east, irrigated areas to the south and vast expanses of unconsolidated and drifting sands to the west. Perennial vegetation is represented by distinct shrub assemblages, responding to variations in topography, geomorphology, drainage and soil and dominated by drought-resistant and/or halophytic shrubs. Outside irrigated areas adjacent to rivers and canals, the study area itself is largely unpopulated except by seasonal pastoralists. Grazing by a local desert breed of sheep (Karakul) is the main and often the only form of desert land-use in the area, representing part of the the most extensive rangeland type in the country which occupies some nine million hectares of the Uzbek portion of the Kyzylkum desert (Machmudov 2006).

Research aims

This thesis is an attempt to fill multiple gaps in our understanding of the biology of Asian houbara populations in Central Asia, with some findings reported for the first time for the species.

Acknowledging livestock breeding as the main form of land-use across most of the houbara's range and taking into account the potentially detrimental effects of grazing on desert vegetation, I aimed to examine whether pastoralism affects houbara distribution and abundance and to assess the impact of livestock on houbara habitat at a landscape scale, focusing on the structure and species composition of perennial vegetation (Chapter 2).

For *in situ* conservation to be successful, it is important to understand what natural and human-related factors affect density and distribution of houbara, and to provide robust estimates of density and regional population size to be used as a basis for future monitoring (Chapter 3).

Nesting productivity is one of the most important components of overall avian productivity, but little is known about its variation within the breeding season, across years and habitats; and nothing is known about how it is affected by habitat characteristics and land-use (Chapter 4).

In the final data chapter, I explore space use and movements of breeding Asian houbara, focusing on home range size, site fidelity and the movements of females with broods as well as adult post-breeding dispersal (Chapter 5).

Finally, in Chapter 6 I acknowledge the key findings and discuss their potential implications for houbara conservation and management and propose future research priorities.

References

Arab News. 2015. Pakistan issues houbara hunting permits to Gulf states dignitaries. Downloaded from: http://www.arabnews.com/news/480571.

Baines, D., Redpath, S., Richardson, M. and Thirgood, S. 2008. The direct and indirect effects of predation by Hen Harriers *Circus cyaneu*s on trends in breeding birds on a Scottish grouse moor. - Ibis 150: 27-36.

Barry, S. and Elith, J. 2006. Error and uncertainty in habitat models. - Journal of Applied Ecology 43: 413-423.

Behnke, R. (ed.) 2006. The socio-economic sauses and consequences of desertification in Central Asia*,* Springer, Dordrecht.

Behnke, R. H., Scoones, I. and Kerven, C. (eds.). 1993. Range ecology at disequilibrium: New models of natural variability and pastoral adaptation of African savannas*,* Overseas Development Institute, London.

Bicknell, J., Smart, J., Hoccom, D., Amar, A., Evans, A. and Et Al. 2010. Impacts of non-native gamebird release in the UK: a review. RSPB Research report no. 40. RSPB, Bedfordshire.

Birdlife International. 2014. Review of the global conservation status of the Asian Houbara Bustard *Chlamydotis macqueenii*. Report to the Convention on Migratory Species Office – Abu Dhabi*,* Cambridge, UK, BirdLife International.

Birdlife International. 2015a. Family Otididae. Downloaded from http://www.birdlife.org on 20/10/2015.

Birdlife International. 2015b. Species factsheet: *Chlamydotis macqueenii*. Downloaded from http://www.birdlife.org on 20/10/2015.

Bock, C. E. and Jones, Z. F. 2004. Avian habitat evaluation: should counting birds count? - Frontiers in Ecology and the Environment 2: 403-410.

Brown, J. L. 1969. The buffer effect and productivity in tit populations. - American Naturalist 103: 347-354.

Burnham, K. P. and Anderson, D. R. (eds.). 2002. Model selection and multi-model inference. A practical information-theoretic approach.*,* Springer, New York.

Burnside, R. J., Carter, I., Dawes, A., Waters, D., Lock, L., Goriup, P. and Szekely, T. 2012. The UK great bustard *Otis tarda* reintroduction trial: a 5-year progress report. - Oryx 46: 112-121.

Butchart, S. H. M., Stattersfield, A. J. and Collar, N. J. 2006. How many bird extinctions have we prevented? - Oryx 40: 266-278.

Butchart, S. H. M., Walpole, M., Collen, B., Van Strien, A. et.al. 2010. Global biodiversity: Indicators of recent declines. - Science 328: 1164-1168.

Cade, T. J. and Temple, S. A. 1995. Management of threatened bird species - evaluation of the hands-on approach. - Ibis 137: S161-S172.

Cahill, A. J., Walker, J. S. and Marsden, S. J. 2006. Recovery within a population of the Critically Endangered citron-crested cockatoo *Cacatua sulphurea citrinocristata* in Indonesia after 10 years of international trade control. - Oryx 40: 161-167.

CBD. 2010. Secretariat of the Convention on Biological Diversity. Global Biodiversity Outlook. Montreal, 155 pages.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M. and Palmer, T. M. 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. - Science Advances 1.

Chargé, R., Sorci, G., Saint Jalme, M., Lesobre, L., Hingrat, Y., Lacroix, F. and Teplitsky, C. 2014. Does recognized genetic management in supportive breeding prevent genetic changes in life-history traits? - Evolutionary Applications 7: 521-532.

Collar, N. J. 1980. The world status of the Houbara: a preliminary review. Proceedings of the Houbara Bustard *Chalmydotis undulata* Symposium. Game Conservancy, Fordingbridge.

Combreau, O., Launay, F. and Lawrence, M. 2001. An assessment of annual mortality rates in adult-sized migrant houbara bustards (*Chlamydotis undulata macqueenii*). - Animal Conservation 4: 133-141.

Combreau, O., Riou, S., Judas, J., Lawrence, M. and Launay, F. 2011. Migratory pathways and connectivity in Asian Houbara Bustards: evidence from 15 years of satellite tracking. - PlosOne 6.

Combreau, O. and Smith, T. R. 1998. Release techniques and predation in the introduction of houbara bustards in Saudi Arabia. - Biological Conservation 84: 147-155.

Côté, I. M. and Sutherland, W. J. 1997. The effectiveness of removing predators to protect bird populations. - Conservation Biology 11: 395-405.

Cummins, B. 2009. Bear country: Predation, politics, and the changing face of Pyrenean pastoralism, Durham, Carolina Academic Press.

Davis, C. 1998. A review of the success of major crane conservation techniques. - Bird Conservation International 8: 19-29.

Dawn News. 2014. Arab royal hunts down 2,100 houbara bustards in three week safari. Downloaded from: http://www.dawn.com/news/1101272.

De Baan, L., Curran, M., Rondinin, C., Visconti, P., Hellweg, S. and Koellner, T. 2015. High-resolution assessment of land use impacts on biodiversity in life cycle assessment using species habitat suitability models. - Environmental Science & Technology 49: 2237-2244.

Del Hoyo, J. and Collar, N. J. 2014. HBW and BirdLife International illustrated checklist of the birds of the world Volume 1: Non-passerines, Barcelona, Lynx Edicions.

Díaz-Fernández, S., Arroyo, B., Casas, F., Martinez-Haro, M. and Viñuela, J. 2013. Effect of game management on wild red-legged partridge abundance. - PlosOne 8: e66671.

Díaz-Fernández, S., Viñuela, J. and Arroyo, B. 2012. Harvest of red-legged partridge in central Spain. - The Journal of Wildlife Management 76: 1354-1363.

Dickens, M. J., Delehanty, D. J. and Romero, L. M. 2010. Stress: An inevitable component of animal translocation. - Biological Conservation 143: 1329-1341.

Dolman, P. M. 2012. Mechanisms and processes underlying landscape structure effects on bird populations. In: Fuller, R. J. (ed.) Birds and habitat: Relationships in changing landscapes. Cambridge University Press.

Dolman, P. M., Collar, N. J., Scotland, K. M. and Burnside, R. J. 2015. Ark or park: the need to predict relative effectiveness of *ex situ* and *in situ* conservation before attempting captive breeding. - Journal of Applied Ecology 52: 841-850.

Dolman, P. M. and Waber, K. 2008. Ecosystem and competition impacts of introduced deer. - Wildlife Research 35: 202-214.

Donald, F. P., Collar, N. J., Marsden, S. J. and Pain, D. J. 2013. The world's rarest birds and the race to save them: 2nd edition, London, Christopher Helm.

Donald, P., Gedeon, K., Collar, N., Spottiswoode, C., Wondafrash, M. and Buchanan, G. 2012. The restricted range of the Ethiopian Bush-crow *Zavattariornis stresemanni* is a consequence of high reliance on modified habitats within narrow climatic limits. - Journal of Ornithology 153: 1031-1044.

Donald, P. F., Sanderson, F. J., Burfield, I. J., Bierman, S. M., Gregory, R. D. and Waliczky, Z. 2007. International conservation policy delivers benefits for birds in Europe. - Science 317: 810-813.

Donazar, J. A. and Fernandez, C. 1990. Population trends of the Griffon vulture *Gyps fulvus* in northern Spain between 1969 and 1989 in relation to conservation measures. - Biological Conservation 53: 83-91.

Doughty, H. L., Karpanty, S. M. and Wilbur, H. M. 2015. Local hunting of carnivores in forested Africa: a meta-analysis. - Oryx 49: 88-95.

Drew, C. A. and Perera, A. 2011. Expert knowledge as a basis for landscape ecological predictive models. In: Drew, C. A., Wiersma, Y. F. and Huettmann, F. (eds.) Predictive species and habitat modeling in landscape ecology. Springer New York, pp. 229-248.

Durant, S. M., Pettorelli, N., Bashir, S., Woodroffe, R. and Et. Al. 2012. Forgotten biodiversity in desert ecosystems. - Science 336: 1379-1380.

Eglington, S. M., Gill, J. A., Smart, M. A., Sutherland, W. J., Watkinson, A. R. and Bolton, M. 2009. Habitat management and patterns of predation of Northern Lapwings on wet grasslands: The influence of linear habitat structures at different spatial scales. - Biological Conservation 142: 314-324.

Elith, J. and Leathwick, J. R. 2009. Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology Evolution and Systematics. Annual Reviews, Palo Alto, pp. 677-697.

Evans, I. M., Summers, R. W., O'toole, L., Orr-Ewing, D. C., Evans, R., Snell, N. and Smith, J. 1999. Evaluating the success of translocating Red Kites *Milvus milvus* to the UK. - Bird Study 46: 129-144.

Fa, J. E., Olivero, J., Farfan, M. A., Marquez, A. L., Vargas, J. M., Real, R. and Nasi, R. 2014. Integrating sustainable hunting in biodiversity protection in Central Africa: Hot spots, weak spots, and strong spots. - PlosOne 9.

Finney, S. K., Pearce-Higgins, J. W. and Yalden, D. W. 2005. The effect of recreational disturbance on an upland breeding bird, the golden plover *Pluvialis apricaria*. - Biological Conservation 121: 53-63.

Frankham, R. 2008. Genetic adaptation to captivity in species conservation programs. - Molecular Ecology 17: 325-333.

Gaucher, P., Paillat, P., Chappuis, C., Saint Jalme, M., Lotfikhah, F. and Wink, M. 1996. Taxonomy of the Houbara bustard *Chlamydotis undulata* subspecies considered on the basis of sexual display and genetic divergence. - Ibis 138: 273-282.

Gill, J. A., Norris, K. and Sutherland, W. J. 2001. The effects of disturbance on habitat use by black-tailed godwits *Limosa limosa*. - Journal of Applied Ecology 38: 846-856.

Gill, J. A. and Sutherland, W. J. 2000. Predicting the consequences of human disturbance from behavioural decisions. In: Gosling, L. M. and Sutherland, W. J. (eds.) Behaviour and Conservation. Cambridge University Press, Cambridge, UK, pp. 51-64.

Goriup, P. D. 1997. The world status of the houbara bustard *Chlamydotis undulata*. - Bird Conservation International 7: 373-397.

Government of the Republic of Kazakhstan. 2014. Decree on the hunting of Asian houbara (in Russian). Astana.

Government of the Republic of Uzbekistan. 2015. Statement: on regulation of the use of biological resources and permission procedures related to their use (In Russian). Tashkent.

Granadeiro, J. P., Dias, M. P., Rebelo, R., Santos, C. D. and Catry, P. 2006. Numbers and population trends of Cory's Shearwater *Calonectris diomedea* at Selvagern Grande, Northeast Atlantic. - Waterbirds 29: 56-60.

Grigoryants, A. A. (ed.) 2010. Red Data Book of Uzbekistan*,* Chinor ENK, Tashkent.

Gubin, B. M. 2004. Drofa-krasotka (Asian Houbara) (in Russian)*,* Almaty Kolor.

Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. - Ecology Letters 8: 993-1009.

Gunnarsson, T. G., Gill, J. A., Appleton, G. F., Gislason, H., Gardarsson, A., Watkinson, A. R. and Sutherland, W. J. 2006. Large-scale habitat associations of birds in lowland Iceland: Implications for conservation. - Biological Conservation 128: 265-275.

Hingrat, Y. and Saint Jalme, M. 2005. Mating system of the Houbara Bustard *Chlamydotis undulata undulata* in eastern Morocco. - Ardeola 52: 91-102.

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart, S. H. M. and et al. 2010. The impact of conservation on the status of the world's vertebrates. - Science 330: 1503-1509.

Iglecia, M. N., Collazo, J. A. and Mckerrow, A. J. 2012. Use of occupancy models to evaluate expert knowledge-based species-habitat relationships. - Avian Conservation and Ecology 7.

Illius, A. W. and O'connor, T. G. 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. - Ecological Applications 9: 798-813.

Islam, M. Z., Basheer, M. P., Shah, M. S., Al Subai, H. and Boug, A. 2012. Captive-breeding and reintroduction of the Asian Houbara Bustard *Chlamydotis macqueenii* in the Kingdom of Saudi Arabia: lessons learned. - International Zoo News 59: 338-360.

IUCN. 2015. The IUCN Red List of Threatened Species.Version 2015-3. http://www.iucnredlist.org downloaded on 05/10/2015.

Jacobs, R. B., Thompson, F. R., Koford, R. R., La Sorte, F. A., Woodward, H. D. and Fitzgerald, J. A. 2012. Habitat and landscape effects on abundance of Missouri's grassland birds. - Journal of Wildlife Management 76: 372-381.

Jensen, H. P., Rollins, D. and Gillen, R. L. 1990. Effects of cattle stock density on trampling loss of simulated ground nests. - Wildlife Society Bulletin 18: 71-74.

Johnson, T. N., Kennedy, P. L., Delcurto, T. and Taylor, R. V. 2011. Bird community responses to cattle stocking rates in a Pacific Northwest bunchgrass prairie. - Agriculture Ecosystems & Environment 144: 338-346.

Jones, C. G., Heck, W., Lewis, R. E., Mungroo, Y. and Cade, T. J. 1995. The restoration of the Mauritius kestrel *Falco punctatus* population. - Ibis 137: s173-s180.

Judas, J., Combreau, O., Lawrence, M., Saleh, M., Launay, F. and Gao, X. Y. 2006. Migration and range use of Asian Houbara Bustard *Chlamydotis macqueenii* breeding in the Gobi Desert, China, revealed by satellite tracking. - Ibis 148: 343-351.

Kamp, J., Oppel, S., Ananin, A. A., Durnev, Y. A., Gashev, S. N., Hölzel, N., Mishchenko, A. L., Pessa, J., Smirenski, S. M., Strelnikov, E. G., Timonen, S., Wolanska, K. and Chan, S. 2015. Global population collapse in a superabundant migratory bird and illegal trapping in China. - Conservation Biology: n/a-n/a.

Kery, M., Royle, J. A. and Schmid, H. 2005. Modeling avian abundance from replicated counts using binomial mixture models. - Ecological Applications 15: 1450-1461.

King, D. I., Chandler, R. B., Collins, J. M., Petersen, W. R. and Lautzenheiser, T. E. 2009. Effects of width, edge and habitat on the abundance and nesting success of scrub-shrub birds in powerline corridors. - Biological Conservation 142: 2672-2680.

Kovshar, A. F. (ed.) 1996. Red Data Book of Kazakhstan, Almaty.

Kuehler, C., Harrity, P., Lieberman, A. and Kuhn, M. 1995. Reintroduction of hand-reared alala *Corvus hawaiiensis* in Hawaii. - Oryx 29: 261-266.

Kuehler, C., Lieberman, A., Oesterle, P., Powers, A. T., Kuhn, M., Snetsinger, T. J., Harrity, P., Tweed, E. J., Fancy, S. G., Woodworth, B. L. and Telfer, T. 2000. Development of restoration techniques for Hawaiian thrushes: Collection of wild eggs, artificial incubation, hand-rearing, captive-breeding, and re-introduction to the wild. - Zoo Biology 19: 263-277.

Lamprey, H. F. 1983. Pastoralism yesterday and today: the overgrazing problem. Bourliere, F., pp. P643-666.

Linklater, W. L. 2003. Science and management in a conservation crisis: A case ctudy with rhinoceros. - Conservation Biology 17: 968-975.

Macdonald, M. A. and Bolton, M. 2008. Predation on wader nests in Europe. - Ibis 150: 54-73.

Machmudov, M. M. 2006. Uzbekistan: country pasture/forage resource profile. FAO.

Marques, T. A., Thomas, L., Fancy, S. G. and Buckland, S. T. 2007. Improving estimates of bird density using multiple-covariate distance sampling. - Auk 124: 1229-1243.

Martin, E., Alonso, J. A., Alonso, J. C. and Morales, M. 1996. Evaluation of captive breeding as a method to conserve threatened Great Bustard (*Otis tarda*) populations. In: Fernandez Gutierrez, J. and Sanz-Zuasti, J. (eds.) Conservacion de las Aves Esteparias y su Habitat. Junta de Castilla y Leon, Valladolid, pp. 131-136.

MEA. 2005. Ecosystems and human well-being: desertification synthesis. World Resources Institute, Washington, DC.

Middleton, N., Stringer, L., Goudie, A. and Thomas, D. 2011. The forgotten billion: MDG achievement in the drylands*,* New York, United Nations Developmetn Programme.

Miller, D. L., Burt, M. L., Rexstad, E. A. and Thomas, L. 2013. Spatial models for distance sampling data: recent developments and future directions. - Methods in Ecology and Evolution 4: 1001-1010.

Milner-Gulland, E. J. and Akçakaya, H. R. 2001. Sustainability indices for exploited populations. - Trends in Ecology & Evolution 16: 686-692.

Milner-Gulland, E. J., Kholodova, M. V., Bekenov, A., Bukreeva, O. M., Grachev, I. A., Amgalan, L. and Lushchekina, A. A. 2001. Dramatic declines in saiga antelope populations. - Oryx 35: 340-345.

Moore, P. 2005. Stock fencing and electric fence exclosures to prevent trampling of Chatham Island oystercatcher *Haematopus chathamensis* eggs, Chatham Island, New Zealand. - Conservation Evidence 2: 76-77.

Mortimore, M., Anderson, S. C., L., Davies, J., Faccer, K., Hesse, C., Morton, J., Nyangena, W., Skinner, J. and Wolfangel, C. 2009. Dryland opportunities: A new paradigm for people, ecosystems and development*,* Gland, Switzerland, IUCN.

Muñoz-Fuentes, V., Green, A. J. and Sorenson, M. D. 2008. Comparing the genetics of wild and captive populations of White-headed Ducks *Oxyura leucocephala*: consequences for recovery programmes. - Ibis 150: 807-815.

Naughton-Treves, L., Holland, M. B. and Brandon, K. 2005. The role of protected areas in conserving biodiversity and sustaining local livelihoods. Annual Review of Environment and Resources, pp. 219-252.

Noer, H. and Secher, H. 1983. Survival of Danish kestrels *Falco tinnunculus* in relation to protection of birds of prey. - Ornis Scandinavica 14: 104-114.

Olaizola, A., Lopez P. 1999. Organization logics of transhumance in Pyrenean sheep farming systems. In: Rubino, R., Mohrand-Fehr, P. (ed.) Systems of sheep and goat production: Organization of husbandry and role of extension services. CIHEAM-IAMZ., Zagarosa, pp. 227-230.

Olson, D. M., Dinerstein, E. D., Wikramanaya, K. E., Burgess, N. D., Powell, G. V. N, Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P. & Kassem, K. R. 2001. Terrestrial ecoregions of the world: a new map of life on earth. - BioScience 51: 933-938.

Oppel, S., Meirinho, A., Ramírez, I., Gardner, B., O'connell, A. F., Miller, P. I. and Louzao, M. 2012. Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. - Biological Conservation 156: 94-104.

Page, G. W., Quinn, P. L. and Warriner, J. C. 1989. Comparison of the breeding of hand- and wild-reared Snowy Plovers. - Conservation Biology 3: 198-201.

Pain, D. J., Martins, T. L. F., Boussekey, M., Diaz, S. H., Downs, C. T., Ekstrom, J. M. M., Garnett, S., Gilardi, J. D., Mcniven, D., Primot, P., Rouys, S., Saoumoe, M., Symes, C. T., Tamungang, S. A., Theuerkauf, J., Villafuerte, D., Verfailles, L., Widmann, P. and Widmann, I. D. 2006. Impact of protection on nest take and nesting success of parrots in Africa, Asia and Australasia. - Animal Conservation 9: 322-330.

Parish, D. M. B. and Sotherton, N. W. 2007. The fate of released captive-reared grey partridges *Perdix perdix*: implications for reintroduction programmes. - Wildlife Biology 13: 140-149.

Pauliny, A., Larsson, M. and Bloqvist, D. 2008. Nest predation management: Effects on reproductive success in endangered shorebirds. - Journal of Wildlife Management 72: 1579-1583.

Pearce-Higgins, J. W., Finney, S. K. and Yalden, D. W. 2007. Testing the effects of recreational disturbance on two upland breeding waders. - Ibis 149: 45-55.

Phillips, S. J., Anderson, R. P. and Schapire, R. E. 2006. Maximum entropy modeling of species geographic distributions. - Ecological Modelling 190: 231-259.

Powell, A. N. and Cuthbert, F. J. 1993. Augmenting small populations of plovers: an assessment of cross-fostering and captive-rearing. - Conservation Biology 7: 160-168.

Puigdefabregas, J. 1998. Ecological impacts of global change on drylands and their implications for desertification. - Land Degradation & Development 9: 393-406.

Pullin, A. S. and Knight, T. M. 2003. Support for decision making in conservation practice: an evidence-based approach. - Journal for Nature Conservation 11: 83-90.

Pullin, A. S., Knight, T. M., Stone, D. A. and Charman, K. 2004. Do conservation managers use scientific evidence to support their decision-making? - Biological Conservation 119: 245-252.

Rabinowitz, A. 1995. Helping a species go extinct: The Sumatran Rhino in Borneo. - Conservation Biology 9: 482-488.

Rachkovskaja, K. and Pereladova, O. 2012. Central Asian southern desert (PA1312). WWF.

Riou, S. and Combreau, O. 2014. Male territories and the lek-like mating system of MacQueen's Bustard *Chlamydotis macqueenii*. - Journal of Ornithology 155: 959-967.

Riou, S., Combreau, O., Judas, J., Lawrence, M., Al Baidani, M. S. and Pitra, C. 2012. Genetic differentiation among migrant and resident populations of the threatened Asian houbara bustard. - Journal of Heredity 103: 64-70.

Riou, S., Judas, J., Lawrence, M., Pole, S. and Combreau, O. 2011. A 10-year assessment of Asian Houbara Bustard populations: trends in Kazakhstan reveal important regional differences. - Bird Conservation International 21: 134-141.

Rushton, S. P., Ormerod, S. J. and Kerby, G. 2004. New paradigms for modelling species distributions? - Journal of Applied Ecology 41: 193-200.

Safriel, U. 2005. Dryland systems. In: Hassan, E. M., Scholes, R. and Ash, N. (eds.) Millenium Ecosystem Assessment. Island Press, Washington, DC.

Saint Jalme, M., Combreau, O., Seddon, P. J., Paillat, P., Gaucher, P. and Vanheezik, Y. 1996. Restoration of *Chlamydotis undulata macqueenii* (Houbara bustard) populations in Saudi Arabia: A progress report. - Restoration Ecology 4: 81-87.

Saiz, H. and Alados, C. L. 2012. Changes in semi-arid plant species associations along a livestock grazing gradient. - Plos One 7.

Sarrazin, F., Bagnolini, C., Pinna, J. L. and Danchin, E. 1996. Breeding biology during establishment of a reintroduced griffon vulture *Gyps fulvus* population. - Ibis 138: 315-325.

Seddon, P. J., Jalme, M. S., Van Heezik, Y., Paillat, P., Gaucher, P. and Combreau, O. 1995. Restoration of houbara bustard populations in Saudi Arabia: developments and future directions. - Oryx 29: 136-142.

Segurado, P. and Araújo, M. B. 2004. An evaluation of methods for modelling species distributions. - Journal of Biogeography 31: 1555-1568.

Sheldon, R. D., Kamp, J., Koshkin, M. A., Urazaliev, R. S., Iskakov, T. K., Field, R. H., Salemgareev, A. R., Khrokov, V. V., Zhuly, V. A., Sklyarenko, S. L. and Donald, P. F. 2013. Breeding ecology of the globally threatened Sociable Lapwing *Vanellus gregarius* and the demographic drivers of recent declines. - Journal of Ornithology 154: 501-516.

Sinclair, A. R. E. and Fryxell, J. M. 1985. The Sahel of Africa: ecology of a disaster. - Canadian Journal of Zoology-Revue Canadienne De Zoologie 63: 987-994.

Skira, I. J., Wapstra, J. E., Towney, G. N. and Naarding, J. A. 1986. Conservation of the short-tailed shearwater *Puffinus tenuirostris* in Tasmania, Australia. - Biological Conservation 37: 225-236.

Smith, R. K., Pullin, A. S., Stewart, G. B. and Sutherland, W. J. 2010. Effectiveness of predator removal for enhancing bird populations. - Conservation Evidence 24: 820-829.

Snyder, N. F. R., Derrickson, S. R., Beissinger, S. R., Wiley, J. W., Smith, T. B., Toone, W. D. and Miller, B. 1996. Limitations of captive breeding in endangered species recovery. - Conservation Biology 10: 338-348.

Sokos, C. K., Birtsas, P. K. and Tsachalidis, E. P. 2008. The aims of galliforms release and choice of techniques. - Wildlife Biology 14: 412-422.

Sullivan, S. and Rohde, R. 2002. On non-equilibrium in arid and semi-arid grazing systems. - Journal of Biogeography 29: 1595-1618.

Sutherland, W. J., Pullin, A. S., Dolman, P. M. and Knight, T. M. 2004. The need for evidence-based conservation. - Trends in Ecology & Evolution 19: 305-308.

Sutter, B. and Ritchison, G. 2005. Effects of grazing on vegetation structure, prey availability, and reproductive success of Grasshopper Sparrows. - Journal of Field Ornithology 76: 345-351.

Teunissen, W., Schekkerman, H., Willems, F. and Majoor, F. 2008. Identifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. - Ibis 150: 74-85.

The Express Tribune. 2015. Smuggled over water: Where there is Houbara Bustards, there is money. Downloaded from: http://tribune.com.pk/story/866650/smuggled-over-water-where-there-is-houbara-bustard-there-is-money/.

Tigar, B. J. and Osborne, P. E. 2000. Invertebrate diet of the Houbara Bustard *Chlamydotis undulata macqueenii* in Abu Dhabi from calibrated faecal analysis. - Ibis 142: 466-475.

Tourenq, C., Combreau, O., Lawrence, M., Pole, S. B., Spalton, A., Gao, X. J., Al Baidani, M. and Launay, F. 2005. Alarming houbara bustard population trends in Asia. - Biological Conservation 121: 1-8.

Tozer, D. C., Nol, E. and Abraham, K. F. 2010. Effects of local and landscape-scale habitat variables on abundance and reproductive success of wetland birds. - Wetlands Ecology and Management 18: 679-693.

UNEP/CMS Secretariat. 2014. A review of migratory bird flyways and priorities for management. CMS Technical Series No. 27. Bonn, Germany. 164 pages.

Urbanek, R. P., Fondow, L. E. A., Zimorski, S. E., Wellington, M. A. and Nipper, M. A. 2010. Winter release and management of reintroduced migratory Whooping Cranes *Grus americana*. - Bird Conservation International 20: 43-54.

van Heezik, Y., Lei, P., Maloney, R. and Sancha, E. 2005. Captive breeding for reintroduction: influence of management practices and biological factors on survival of captive kaki (black stilt). - Zoo Biology 24: 459-474.

van Heezik, Y. and Ostrowski, S. 2001. Conservation breeding for reintroductions: assessing survival in a captive flock of houbara bustards. - Animal Conservation 4: 195-201.

Vaughan, C., Nemeth, N. M., Cary, J. and Temple, S. 2005. Response of a Scarlet Macaw *Ara macao* population to conservation practices in Costa Rica. - Bird Conservation International 15: 119-130.

Vié, J.-C., Hilton-Taylor, C. and Stuart, S. N. (eds.). 2009. Wildlife in a changing world – an analysis of the 2008 IUCN Red List of threatened tpecies*,* IUCN, Gland, Switzerland.

Waber, K., Spencer, J. and Dolman, P. M. 2013. Achieving landscape-scale deer management for biodiversity conservation: The need to consider sources and sinks. - Journal of Wildlife Management 77: 726-736.

Watson, J. E. M., Dudley, N., Segan, D. B. and Hockings, M. 2014. The performance and potential of protected areas. - Nature 515: 67-73.

Wiemeyer, S. N. 1981. Captive propagation of bald eagles at Patuxent Wildlife Research Center and introductions into the wild. - Raptor Research 15: 68-82.

Williams, J. B. and Tieleman, B. I. 2005. Physiological adaptation in desert birds. - BioScience 55: 416-425.

Williams, S. E. and Hoffman, E. A. 2009. Minimizing genetic adaptation in captive breeding programs: A review. - Biological Conservation 142: 2388-2400.

Zapata-Rios, G., Urgiles, C. and Suarez, E. 2009. Mammal hunting by the Shuar of the Ecuadorian Amazon: is it sustainable? - Oryx 43: 375-385.

Zwank, P. J. and Wilson, C. D. 1987. Survival of captive, parent-reared Mississippi Sandhill Cranes released on a refuge. - Conservation Biology 1: 165-168.

Chapter 2

Do sheep affect distribution and habitat of Asian Houbara *Chlamydotis macqueenii*?

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Abstract

We examined whether pastoralism affected the distribution of Asian Houbara Bustard *Chlamydotis macqueenii* (IUCN Vulnerable) or modified its habitat across 14,500 km^2 of the Kyzylkum Desert, Uzbekistan. In this landscape, sheep grazing is constrained by access to water, allowing effects to be examined independent of topography and vegetation community. Across a gradient of sheep density (0–10 to 30–80 individuals km^{-2}) we achieved n = 140 10-km driven transects (total driven 3,500 km). On all transects Houbara and sheep were surveyed at least once, and 96 were driven three times with vegetation sampled on four 50 m-long transects along each of these (measuring 7,493 shrubs). Houbara distribution and abundance was also recorded at 147 point counts. In Generalised Linear Models that controlled for plant community, neither interpolated sheep density (within 1 km buffers) nor topographic variation affected houbara incidence on transects, or incidence and abundance at point counts. Although subtle effects were found for some palatable shrubs, sheep did not strongly modify shrub composition or structure at landscape scales. At landscape-scales, livestock browsing has not widely degraded these rangelands, which appear sustainably managed or even under-utilised. Pastoralism and houbara conservation may therefore be compatible, although impacts on nesting females require investigation.

Introduction

In the deserts and semi-arid rangelands of Central Asia, strong evidence exists for vegetation degradation through over-exploitation by livestock, notable up to 3 km and detectable up to 5 km around watering points or villages (Behnke et al. 2006, Coughenour et al. 2006). However, the effects of pastoralism on rangeland condition at landscape and regional scales remain ambiguous (Stringer 2006), since reduced infrastructure and management capacity in the post-Soviet era has resulted in the under-utilisation or complete abandonment of some extensive rangelands remote from settlements (Coughenour et al. 2006, Shaumarov et al. 2012). We used the opportunity provided by this variation in sheep density to conduct a quasi-experimental landscape-scale study of the consequences of livestock browsing and pastoralism, both for shrub desert condition and for the distribution of Asian Houbara Bustard *Chlamydotis macqueenii* (IUCN Vulnerable).

Breeding populations of the Asian Houbara have declined substantially across its range, encompassing the Arabian Peninsula northwards to Central Asia and east to China (Riou et al. 2011, BLI 2012). Arab falconers prize both the Asian and the closely related African Houbara *C. undulata* as their main quarry; in addition to their cultural significance, these species have considerable economic value to host countries across range states (Bailey et al. 1998). Population declines, especially in the Asian species, have primarily been driven by unregulated hunting throughout the wintering range (Tourenq et al. 2005, Riou et al. 2011). Reducing the impacts of hunting on wild populations is fundamental to ensuring both species' survival, but concern has also been expressed over the deleterious effects of livestock grazing, both indirectly through deterioration in habitat quality and directly through impacts on breeding populations (Lavee 1988, Osborne et al. 1997, Le Cuziat et al. 2005b). Management to enhance productivity by mitigating habitat deterioration has the potential to contribute to a sustainable future for these species.

Sheep and goats are thought to affect houbara distribution and decrease productivity through disturbance of nesting females by shepherds and their dogs and nest trampling by flocks (Lavee 1988). The dominant shrub species are palatable to sheep but also provide houbara with food (Gubin 2004, Hingrat et al. 2007b) and concealment (van Heezik and Seddon 1999, Hingrat et al. 2007a). Therefore, as livestock can reduce shrub biomass, productivity, density and structure, and alter the plant composition of shrub desert vegetation (Behnke 2006, Saiz and Alados 2012), pastoralism is also suspected of modifying habitat suitability for houbara. Numbers of African Houbara increased with distance from wells (a proxy for nomadic pastoralism and associated human disturbance) in semi-arid shrub vegetation in the Middle Atlas Mountains, Morocco, during the breeding season (Le Cuziat et al. 2005a), suggesting that pastoralism influences houbara distribution. However, whether this is through habitat degradation, disturbance, persecution or a combination of these factors is not clear. It is also unclear whether findings concerning the African Houbara can be assumed to apply to the Asian species, given that the nature of pastoralism may differ between the continents. In view of the importance of pastoralism to local livelihoods and the national economies of semi-arid range states (FAO 2006, Lindt 2006), a robust evidence base is clearly needed to inform any initiatives to mitigate population declines through habitat management (Sutherland et al. 2004).

Acknowledging the potential tension between local over-exploitation and wider under-utilisation of rangelands, we examined the distribution of Asian Houbara, variation in sheep density and the structure of desert shrub vegetation in a well-replicated and extensive study across approximately 14,500 km^2 of potentially suitable habitat in the Kyzylkum Desert in Uzbekistan. Our aims were (i) to examine whether utilisation of semi-arid shrub desert by pastoralists affected houbara distribution and abundance and (ii) to assess the impact of livestock on houbara habitat at landscape rather than more localised scales, focusing on shrub structure and relative species composition.

Methods

2.1. Study area

The study area (39.34–40.56°N 62.21–65.20°E, altitude 170–400 m above sea level) was located in the Bukhara District of Uzbekistan, within the Kyzylkum Desert of the southern Central Asian desert ecoregion (Olson et al. 2001) (Fig.1). The climate is characterised by variably cold winters (mean monthly temperatures 0–5°C, but often reaching –25°C), hot summers, and an annual precipitation of 125–170 mm, mostly during winter and spring (as snow and rain). The landscape is predominantly flat, with undulating terrain, bounded by mountain ranges to the north and east. Variations in topography, geomorphology, drainage and soil result in areas with distinctly different shrub-desert communities, all dominated by drought-resistant and or halophytic shrubs. Following Rachkovskaya (1995), we classified these plant communities as: (a) '*Artemisia*' (4,400 km²), located on gypseous soils on a piedmont slope at 200–400 m elevation intersected by wadis, dominated by *A. diffusa*; (b) '*Salsola*' (3,500 km²), on halophytic soils dominated by *S. arbuscula*, *S. gemmascens* and *S. rigida*; (c) '*Astragalus*' (1,860 km²) on semi-consolidated sands, dominated by *A. villosissimus* and *Convolvulus hamadae* but also containing *Salsola* spp. and *Artemisia diffusa*; and (d) '*Calligonum*' (4,730 km²) on areas of weakly consolidated sands, supporting a diverse shrub community typified by *Calligonum* spp. Owing to logistical difficulties surveys were not continued in an extensive area (7,700 km²) of unconsolidated dunes to the west of the study area that supported White Saxaul *Haloxylon persicum* subforest with abundant Sandy Acacia *Ammodendron conollyi*; however, no houbara and few pastoralists were detected during pilot work in this habitat. Ephemeral plants occurred sparsely throughout all plant communities; additionally a thin ground cover of grasses and or *Carex* occurred in spring on gypseous soils and semi-consolidated sands (*Artemisia* and *Astragalus* vegetation respectively).

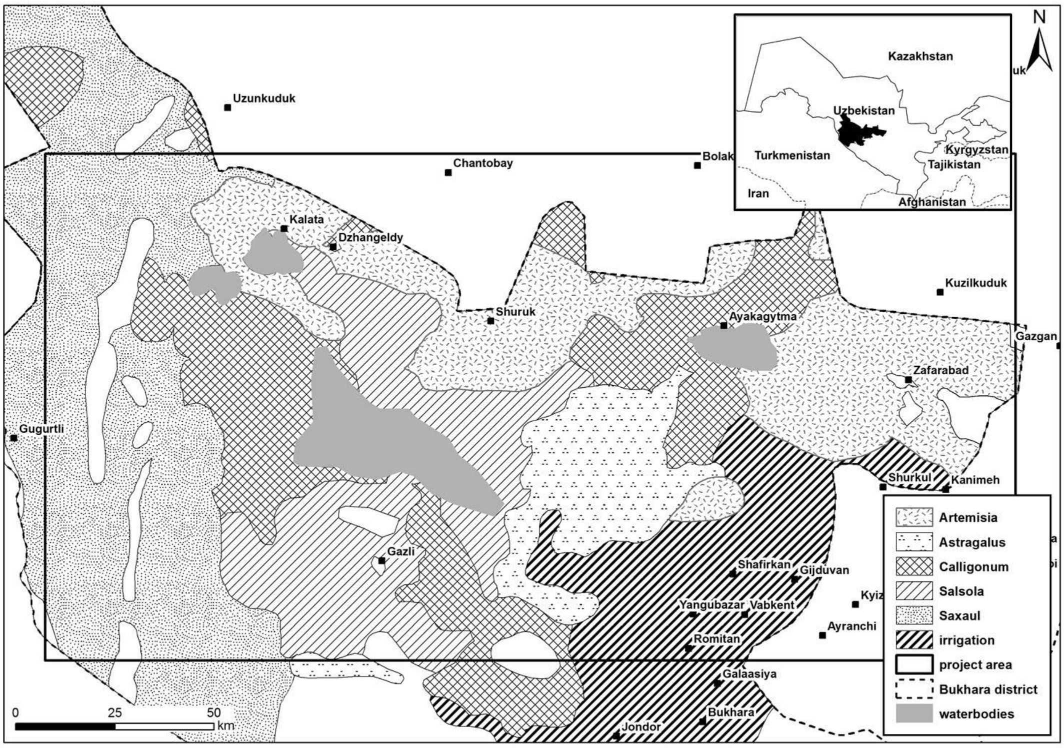

Fig. 1. Study area within Bukhara District, Uzbekistan, showing distribution of desert plant communities within it, following Rachkovskaya (1995). In the map inset, Bukhara District is shown in black.

The south-east of the study area borders irrigated croplands and permanent settlements (Fig.1), but the study area itself is unpopulated except by seasonal pastoralists, who graze Karakul sheep and smaller numbers of goats. These are brought into the desert for lambing during the spring (April–June), coinciding with the breeding and nesting season of Asian Houbara, when ephemeral plants and some perennial shrubs provide high-quality fodder; they are removed to irrigated areas and the vicinity of canals and settlements during June. During the spring period most of the sheep are managed out of seasonal camps, comprising a watering point and either small clay huts or mobile caravans, and often holding several hundred sheep each. In addition to spring grazing, limited areas of *Artemisia* vegetation are utilised throughout the year by pastoralists from piedmont villages (Kalata, Dzhangeldy, Shuruk, Ayakagytma); thus grazing impacts were expected to be greatest in this plant community. Sheep distribution during spring is therefore limited by the distribution of functional wells or to areas to which water can be transported; this leaves extensive areas of desert relatively unutilised, and permitted us to examine the effects of sheep density independently of plant community.

2.2. Sampling of sheep, houbara density and vegetation

In Central Asia, the localised impacts of sheep grazing on semi-arid vegetation are detectable by remote sensing up to 3.5–5 km from settlements, and to a lesser distance around wells (Behnke et al. 2006, Coughenour et al. 2006). In our study area, in addition to localised degradation in the immediate vicinity of watering points or sheep camps, where palatable shrubs are absent and unpalatable *Peganum harmala* can be dominant, sheep density also varied at landscape scales. Shrub desert within 10–20 km of the cropland and settlement boundary contained numerous seasonal sheep camps, with a mean distance between camps of 2.3 km, $SD = 1.2$, such that all intervening desert was subjected to grazing. Further from settlements or permanent water, the density of camps was lower, and in the remotest areas few pastoralists were encountered. We used this landscape-scale variation in the livestock density to relate houbara presence/abundance and shrub desert composition to sheep density, stratified across plant communities.

Houbara and sheep were simultaneously surveyed along 140 10-km driven transects, during the period of houbara display and breeding, from mid-March to mid-

June 2012. Numbers of 10-km transects were similar among three of the four plant communities sampled (*Artemisia*, n = 39; *Salsola*, n = 41; *Astragalus*, n = 34), but *Calligonum* (n = 26) vegetation received lower sampling effort owing to the rougher terrain and denser vegetation. Given that sheep and goats were both browsing shrub vegetation in the same way, that goats were always found in mixed flocks with sheep dominating, and that it was impracticable to separate them reliably when counting distant flocks, we combined observations of both species for analysis and hereafter refer to both as 'sheep'.

Transects were at least 2 km apart and were arranged so as not to cross plant community boundaries. We aimed to drive each transect once in each of the three periods 22 March–22 April, 4 May–5 June and 7–19 June. Owing to time restrictions, 96 transects were run three times, 18 twice and 26 once, totalling 3,500 km. Surveys were restricted to 2–3 hours after sunrise and before sunset, when houbara are most active (Combreau and Launay 1996). Sheep were out in the desert from early in the morning till sunset and did not return to camps or wells during the day, sometimes for 2 days. A vehicle with one driver and one observer was driven off-road at an average speed of 15 km/h, scanning with the naked eye for houbara and sheep. For each houbara or houbara group observed we recorded a GPS waypoint of the detection on the transect line, distance (measured using a laser range-finder effective up to approximately 1.2 km), angle from transect line (using a compass) and number of individuals; where possible, individuals were sexed (by plumage and morphological features) and aged (adult or juvenile, defined as young of the year). Flying birds often could not be sexed but were included in the density analysis as they were considered to have flushed from the ground at the approach of the vehicle; perpendicular distance was measured to the equivalent location on the ground. For each sheep flock, the number of individuals was counted (using binoculars), and the perpendicular distance from the transect line to the flock centre, following Buckland et al. (2001), was measured by laser range-finder. All sheep camps located during survey work in the study area were mapped using a hand-held GPS.

Houbara were also surveyed at 147 point counts (that were at least 3 km apart), conducted during 14 April–5 June (of which 38 were repeated once), stratified across plant communities (*Artemisia*, n = 43; *Salsola*, n = 52; *Astragalus*, n = 42; *Calligonum*, n = 10). Point counts lasted 30 minutes and were conducted within 2–3 hours after sunrise and before sunset using telescope and binoculars. For each houbara observed, we recorded: sex, age, number of individuals and the radial distance from the observer (measured by laser range-finder, except for a few observations >1,200 m which had to be estimated by eye owing to strong heat haze and bearing against bright sun). The few houbara seen flying were usually moving in response to interactions with other houbara (usually moving short distances and still visible on landing) and were therefore included in the distance analysis.

Species composition and structure of shrub vegetation were measured on 96 of the 10-km transects during the final transect round, between 3 and 19 June, after any effects of spring browsing on fresh growth had accumulated. Vegetation was recorded at four locations spaced along each 10-km transect; and Houbara survey was then discontinued for the first 500 m of driving after sampling vegetation. At each location, a 50 m line intercept transect was conducted, following Rich et al. (2005), recording the species, height (measured with a ruler to 1 cm accuracy) and diameter of each shrub touching the line. Shrub height was used in further analysis as an index of shrub volume, as it was strongly correlated with diameter (r = 0.592, p = 0.001). Recorded frequency of shrubs (number per 50 m) increases with greater shrub density, but also with greater size of individual shrubs that are thus more likely to intercept a line placed at fixed distance from their rooting point; it should therefore be considered an index of shrub cover. Shrub species were identified from Gintzburger et al. (2003), and validated by two botanists with extensive experience of the Kyzylkum. Within the study area, shrub composition is broadly homogeneous over large areas owing to the combined effects of landform and substrate (clay foothills, saline outwash plain, areas of accumulated sand: Fig.1), and density is also consistent over scales greater than 10 km; four line intercepts were therefore considered sufficient to represent vegetation on each transect. For analysis, data from the four line intercepts were pooled for each 10 km driven transect (providing the mean number or height of each species per 200 m).

2.3. Analysis

2.3.1. Distance analysis of sheep and houbara density

Sheep and houbara densities were estimated by distance analysis conducted in DISTANCE 6.0. For sheep, distance transects were two-sided (sampling fraction 1.0) and for the (highly cryptic) houbara the sampling fraction on distance transects was estimated to be 0.7 (owing to reduced search capacity on the driver's side of the vehicle); for houbara on point counts the sampling fraction was specified as 1.0. For those distance transects driven three times (n = 96) similar numbers of houbara groups were observed per transect among each of the three survey periods (generalised linear model with Poisson error, controlling for transect ID: period $X^2 = 1.807$, $p = 0.405$; transect ID, $X^2 = 44.697$, $p = 0.180$). Repeat surveys were considered as replicate observations and were used to calculate transect-specific mean densities.

For both line transects and point counts, Uniform, Half-normal and Hazard-rate detection functions, examining both cosine and polynomial adjustments (simple or hermite), were fitted following Buckland et al. (2001). The detection model with the lowest Akaike Information Criterion adjusted for finite sample size (AICc) was selected; when there were two or more best competing models (with $⊿AIC <2$), model-averaging was undertaken in DISTANCE, with variance estimated by bootstrapping (600 iterations). On transects, birds were detected to a maximum distance of 1,000 m (mean = 207 m, *SD* ± 166), and perpendicular distances of all observations were measured by laser range-finder. Separate sets of models were examined after truncation of either 5% or 10% of the most distant observations, following Buckland et al. (2001), and whichever provided the narrowest confidence intervals to density was selected. For point counts, displaying males could be detected beyond 2 km. However, observations were truncated at 1,000 m to use only those with radial distance confirmed by laser range-finder, as error in distance estimates makes density estimates unreliable (Buckland et al. 2001). In predicting density, the mean observed group size was used if the regression of group size against perpendicular distance was $p >0.15$; otherwise adjusted group size was used.

The null hypothesis that densities (of sheep and houbara) were similar among the four plant communities was tested by Analysis of Variance performed on point count and transect-specific density estimates, with plant community treated as a fixed effect.

2.3.2. Effects of sheep density on houbara

To examine the effects of sheep density on houbara incidence and local density we constructed a series of Generalised Linear Models (GLMs). The first of these compared characteristics of locations at which houbara were observed on distance transects to those of random points, in a used-available design (Manly et al. 2002) with binomial error and log link. We excluded four individuals recorded on the second or third transect round which occurred within 1.5 km of a previous observation, to avoid any pseudoreplication by individual. Random points were generated within a polygon enclosing all driven transects (buffered by 5 km), and excluding unsuitable areas (drainage marsh and mountains), conducted in ArcMap 10.1. The second GLM examined incidence at point counts (0: absence both visits, 1: presence on one or more visits) with binomial error and log link, controlling for number of repeat surveys (1 or 2) as a covariate. The third considered abundance at point counts (number of individuals observed within 1 km radius or, for points with two visits, the maximum count on a single visit), again controlling for number of visits, with negative binomial error and log link (as models with Poisson error were over-dispersed).

Sheep density information was available for the driven transects. To allow sheep density to be estimated for other locations (including point counts and random points), we assigned transect-specific sheep values to transect centroids, and created an interpolated surface by Inverse Distance Weighting (with 500 m raster resolution) using ArcMap 10.1. Mean sheep density was then extracted from 1 km radius buffers around each location (observations on transects, random points and point counts). Interpolated sheep density within a buffer of 2.5 km around transects was validated against the number of sheep camps mapped within the same buffers, by Pearson's correlation coefficient.

In each of the three sets of GLMs, before testing for the effects of sheep density, we first constructed a series of alternative plausible models of environmental effects on houbara incidence or abundance. *Artemisia*-dominated vegetation occurs at higher elevations ($F_{3,125} = 60.42$, $p = 0.001$, $R^2 = 0.592$; Tukey $p < 0.001$) than all other plant communities, which occur at similar elevations to each other ($p > 0.05$); this precluded inclusion of elevation and vegetation together in models. We a priori considered plant community to be more likely to explain houbara incidence or abundance, particularly given the low elevation range encountered in the study area. Previous studies have found the distribution of African Houbara (Le Cuziat et al. 2005a, Carrascal et al. 2008) or other bustards (Moreira 2004, Silva et al. 2004, Alonso et al. 2012) to be related to topography. We therefore examined the effects of rugosity, measured as the standard deviation (*SD*) of digital elevation (ASTER GDEM V2, spatial resolution 30 m) (METI and NASA 2011) extracted from 1 km radius buffers around observations or random points. A 1 km radius was considered appropriate, as 50% kernel home ranges of male African Houbara during the breeding season vary from 0.1 to 4 km^2 (mean = 1, *SD* = 1) (Hingrat et al. 2004). Rugosity within buffers was significantly but only weakly related to plant community (transect presence/absence locations: $F_{3,142} = 10.79$, $p = 0.001$, $R^2 = 0.168$; point counts: $F_{3,144} = 17.83$, p = 0.001, $R^2 = 0.256$), which allowed both predictors to be included in multivariate models (Freckleton 2002). The most strongly supported environmental models were selected by comparing AICc, those within 2 AICc units having similar support (Buckland et al. 2001). For the selected environmental models, we then included a term for mean interpolated sheep density, extracted from a 1 km buffer around the observation point, tested by examining the change in AICc (⊿*AICc*) relative to the equivalent base model.

2.3.3. Associations between sheep density, shrub composition and vegetation structure

A total of 28 shrub species were recorded on vegetation line intercepts; for analysis of the effects of sheep density, 10 rare species recorded on <5% of 10-km transects were omitted, allowing us to include species identity in models of shrub height or frequency. We categorised shrub species according to their palatability to sheep (as: high, medium or low), following information in Gintzburger et al. (2003) (see Appendix 1). Shrub palatability was coded separately between spring/summer and autumn/winter, because green growth of some species is unpalatable but dried stems or seed-heads are eaten in autumn and winter. In analysis of species' intercept frequency we considered palatability coded across all seasons, as cumulative effects of browsing in any season may reduce overall shrub density and cover. However, for analysis of shrub height (a measure of that year's fresh growth remaining in June), we considered palatability in spring and summer only (Appendix 1).

Separately for each shrub palatability class, species- and transect-specific measures of (a) shrub frequency (total number of shrubs on four line intercepts, treating a zero as the measure for that transect) and (b) mean shrub height (averaged across four intercepts, treating transects for which the species was not recorded as missing data), both square-root transformed to satisfy homogeneity of variance, were related to transect-specific sheep density (individuals km^{-2}, square-root transformed) by GLMs, with normal error, controlling for species and plant community (as the marked edaphic differences may affect productivity of those species occurring across more than one plant community). The most abundant shrub species within each palatability class were also modelled separately, relating mean frequency and height per transect to transect-specific sheep density (square-root transformed).

All statistical models were constructed in PASW Statistics 18 (SPSS_Inc 2009).

Results

On driven transects, 83 individuals or small groups of houbara were observed, comprising 113 adults and 14 juveniles. Of the adults, 54% were flying, 29% walking, 10% displaying, 5% crouching and 2% standing when detected. Of the adults that could be sexed ($n = 79$, 70%), 70% were male; females were considered to have been under-recorded, as they are generally more cryptic than males in the breeding season and many were incubating during the survey periods. For analysis of transects all observations of adult birds were used. Houbara group size did not differ among plant communities ($F_{3,79} = 1.029$, $p = 0.385$; all Tukey $p > 0.5$) and was therefore pooled for subsequent distance analysis. To estimate adult density we adjusted for the observed proportion of males and multiplied by two, assuming a 50:50 sex ratio, following Combreau et al. (2002).

At point counts, 145 individuals or groups of houbara were recorded, comprising 153 adults and three juveniles. Of the adults, 36% were displaying, 34% standing, 20% walking, 5% flying and 5% crouching when detected. Again, houbara group size did not differ among plant communities ($F_{3,141} = 0.230$, $p = 0.875$; all Tukey >0.5). Of the adults, most (86%) could be sexed; of these 93% were males. The detectability of males was greater than that of the highly cryptic females owing to males' larger size, interactive behaviour and display. Known females were therefore excluded from further analysis of point counts. The mean distance (square-root transformed) did not differ between males ($n = 124$) and unsexed birds ($n = 20$) ($t_{136} = 1.8$, $p = 0.93$). We therefore pooled males and unsexed birds for subsequent analysis, adjusting for the proportion of males and again multiplying by two to estimate adult density.

For houbara observations both on transects (after truncating 5% of the most distant observations) and at point counts (truncated at 1,000 m), Half-normal and Uniform models with cosine adjustments provided the best model fit, with a mean

Effective Strip Width (ESW) of 108 m (95% CI; 84–137) and an Effective Detection Radius (EDR) of 1,000 m (95% CI; 1,000–1,000), respectively.

On driven transects a total of 299 sheep groups were observed, with mean group size of 158 (*SD* 132.4, range 1–680). Sheep group size (square-root transformed) was similar among plant communities (after truncating 10% of the most distant observations: $F_{3,263} = 1.514$, $p = 0.211$; all Tukey >0.05) and the observed mean was therefore used in subsequent analysis. Perpendicular distances to observed sheep flocks did not differ among plant communities (data truncated at 10%; $F_{3,263} = 1.514$, $p = 0.211$, all Tukey p >0.05); therefore detectability was pooled. After truncation, Half-normal, Uniform and Hazard-rate with cosine adjustment and Uniform with simple polynomial adjustment provided the best-fitting models, with an ESW of 422 m (95% CI; 374–476). Sheep density extracted from interpolated density surface within 2.5 km transect buffers was positively correlated with the density of sheep camps mapped within the same buffers ($r = 0.789$, $n = 142$, $p = 0.001$).

Sheep density varied spatially (Fig.2), and was low (0–10 individuals km^{-2}) or moderate (10–30 individuals km^{-2}) across large areas (7,500 km² and 5,500 km² respectively). In rangelands with access to water, however, densities reached 30–83 individuals km^{-2} (on 1,500 km² of the study area). Mean sheep density differed among plant communities ($F_{3,\ 137} = 26.16$, $p = 0.001$, $R^2 = 0.350$; Tukey $p < 0.05$), being more than three times higher in *Astragalus*, with *Artemisia*, *Salsola* and *Calligonum* communities having similar sheep densities (Tukey $p > 0.05$). However, considerable variation within each plant community permits the independent effects of sheep density to be examined (Fig.3); for example, within *Artemisia*-dominated vegetation 11 transects had medium-high sheep density (5–35 individuals km^{-2}) while 13 had low density (0–5 individuals km^{-2}).

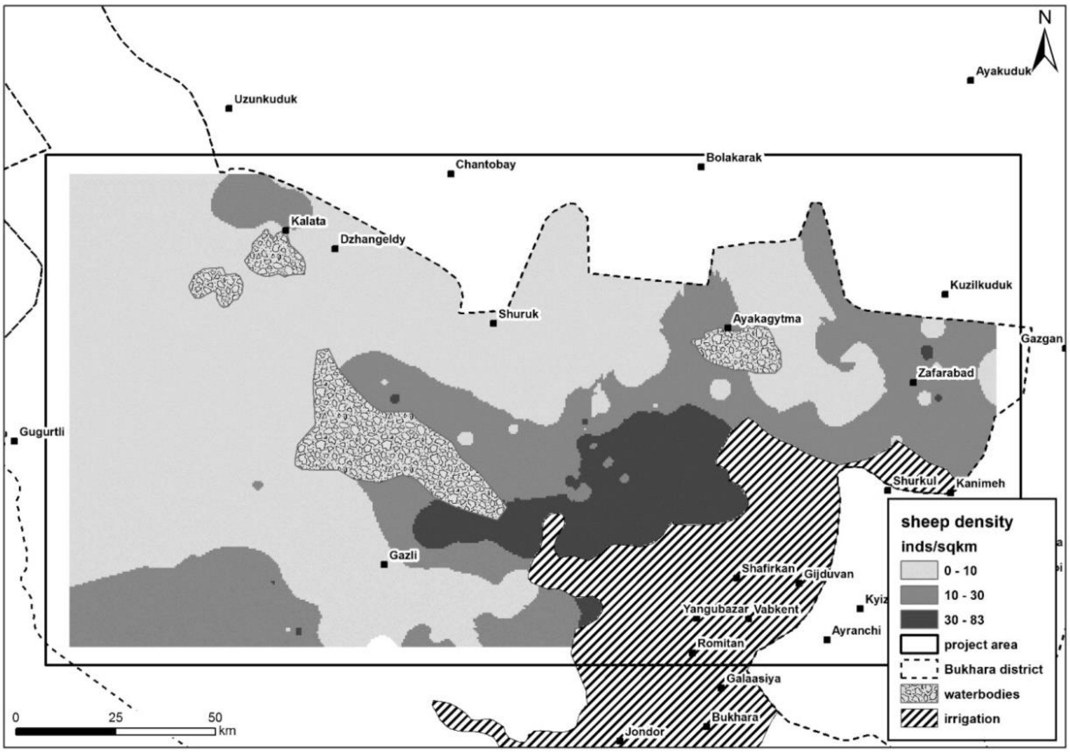

Fig. 2. Sheep density surface for the study area in Bukhara District, Uzbekistan, created by interpolation of transect-specific densities (assigned to transect midpoints). Density interpolation is limited to the area covered by driven transects and within which sheep camps were mapped.

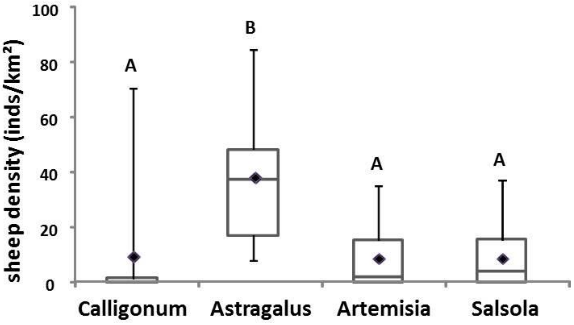

Fig. 3. Sheep density among four plant communities, based on transect-specific density, showing the median (horizontal line), quartiles and range (bars); means (diamonds) that share a superscript do not differ (Tukey test, $p > 0.05$).

3.1. Effect of sheep density on houbara abundance and distribution

Houbara density appeared lower in the *Calligonum*-dominated plant community (Fig.4) but, owing to wide confidence intervals on density estimates, did not differ significantly among the four plant communities either at point counts ($F_{3,143} = 1.370$, $p = 0.254$) or on transects ($F_{3,137} = 1.374$, $p = 0.253$). Sheep density was similar between areas where houbara were observed on transects (*n* = 70, mean = 17.1 individuals km^{-2}, *SE* = 2.1) and random locations (*n* = 120, mean = 14.5, *SE* = 1.4; *t* = 1.054, *p* = 0.294).

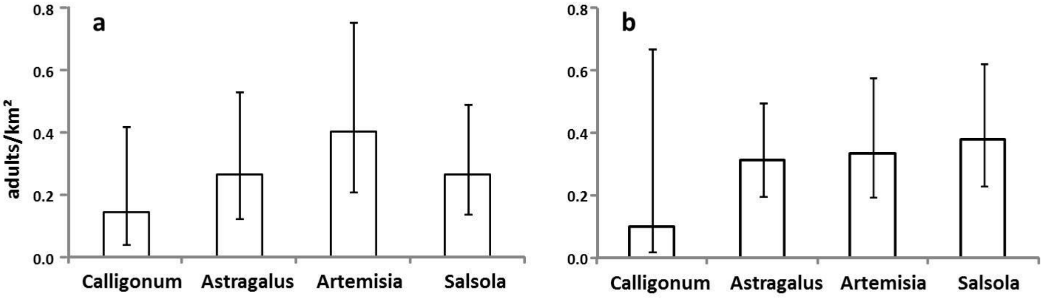

Fig. 4. Estimated mean density of adult houbara from (a) transects and (b) point counts in Bukhara District within four plant communities, showing 95% CI (bars). Adult density was estimated from transect-specific and point count-specific density, then multiplied by the proportion of males among observed adults, and then by 2, assuming a 50:50 sex ratio, following Combreau et al. (2002).

In light of the smaller sample size in *Calligonum* vegetation, and low number of houbara observations, Generalised Linear Models to analyse the relation between houbara and sheep density were only constructed using observations from the remaining three vegetation types. There was no strong support for an effect of desert shrub community or landscape rugosity on either incidence or abundance of houbara in any of the environmental models (Table 1 A–D). Incorporating a term for sheep density into these base models gave no evidence that sheep density affected houbara incidence on transects (Table 1 A, B). Surprisingly, there appeared to be some support for a positive effect of sheep density on probability of houbara incidence on point counts, but only for models that did not control for plant community (Table 1 C). Models of houbara abundance at point locations gave no support for an effect of sheep density when compared to environmental base models (Table 1 D).

Table 1. Generalised Linear Models of houbara distribution, examining houbara incidence on transects compared to random points (used/available design with binomial error), for (A) all adults (*n* = 64; random *n* = 120), and (B) males only (*n* = 26, random *n* = 60); (C) houbara incidence at point counts (present on one or more visits, *n* = 64, absent *n* = 74;with binomial error, controlling for repeat visits); (D) houbara abundance at point counts (*n* = 114, negative binomial error, controlling for repeat visits). For each dependent variable (A, B, C, D), alternative environmental models that consider one or both of topographic rugosity and plant communities ('veg': 3 categories, excluding *Calligonum*) and the null model (intercept-only) are compared by their relative AICc (ΔAICc); models within 2 AICc units of the best-supported model are considered equally plausible. For each dependent variable (A–D), the effect of sheep density is tested by its addition to the supported environmental models, with ΔAICc (relative to the corresponding environmental base model, in the same table row) showing the effect of sheep density. Values in bold represent strong support (ΔAICc < -2.0).

	Models of environmental variables only						**Baseline environmental models plus test of sheep density effect**					
	Model	**Predictor**	**df**	***B (SE)***	**AICc**	**ΔAICc**	**Model**	**Predictor**	**df**	***B (SE)***	**AICc**	**Δ AICc**
A) Transects, adults, incidence	1	rugosity	1	0.019 (0.05)	165.588	**1.415**	1+sheep	rugosity	1	–0.010 (0.02)	163.958	–1.630
								sheep D	1	0.211 (0.18)		
	2	veg	2		166.250	2.077						
	3	veg	2		167.024	2.851						
		rugosity	1	0.003 (0.05)								
	4	intercept		–0.135 (0.17)	164.173	**0**	4+sheep	Intercept	1	0.158 (0.21)	162.478	–1.695
								sheep D	1	0.018 (0.07)		
B) Transects, males, incidence	5	rugosity	1	–0.004 (0.07)	137.345	2.082						
	6	veg	2		137.626	2.363						
	7	veg	2		139.601	4.338						
		rugosity	1	–0.040 (0.08)								
	8	intercept	1	0.228 (0.20)	135.263	**0**	8+sheep	Intercept	1	–0.105 (0.10)	136.287	+1.124
								sheep D	1	0.574 (0.39)		
C) Point counts, incidence	9	rugosity	1	0.012 (0.06)	195.099	**1.664**	9+sheep	rugosity	1	0.050 (0.07)	192.553	**–2.546**
								sheep D	1	0.025 (0.01)		
	10	veg	2		192.741	**0**	10+sheep	veg	2		194.266	+1.525
								sheep D	1	0.015 (0.01)		
	11	veg	2		193.223	**0.482**	11+sheep	veg	2		194.690	+1.467
		rugosity	1	0.106 (0.08)				rugosity	1	0.109 (0.08)		
								sheep D	1			
	12	intercept	1	–0.251 (0.35)	193.042	**0.301**	12+sheep	Intercept	1	–0.662 (0.41)	190.926	**–2.116**
								sheep D	1	0.023 (0.01)		
D) Point counts, abundance	13	rugosity	1	–0.107 (0.06)	291.720	**0**	13+sheep	rugosity	1	–0.124 (0.06)	292.911	+1.191
								sheep D	1	–0.074 (0.07)		
	14	veg	2		296.933	5.213						
	15	veg	2		294.688	2.968						
		rugosity	1	–0.145 (0.07)								
	16	intercept	1	0.038 (0.27)	292.906	**1.186**	16+sheep	Intercept	1	0.144 (0.37)	294.836	+1.930
								sheep D	1	–0.031 (0.07)		

3.2. Association between sheep density, shrub frequency and height

A total of 7,493 shrubs were measured along 19.2 km of walked line intercepts, providing data for 96 of the 10-km transects across a wide range of sheep density (mean of 78.7 shrubs, *SD* = 35.1, range 24 to 190 shrubs, per 10-km transect). On transects with greater sheep density, we recorded a greater frequency of shrubs of highly palatable species (controlling for plant community and individual shrub species, $n = 7$; Table 2, A). No relationship was found between sheep density and the frequency of shrubs of medium ($n = 6$) or low palatability ($n = 5$). When we examined the frequency of individual shrub species, considering the most abundant species of high (*Alhagi pseudalhagi*, *Artemisia diffusa* and *Salsola arbuscula*) or medium palatability (*Convolvulus hamadae* and *Astragalus villosissimus*), no reductions in shrub frequency at higher sheep density were found (Table 2 A); rather, a positive association was supported for *Artemisia diffusa*. This model controlled for plant community; however, as the abundance of *Artemisia* is greatest in the *Artemisia*-dominated community we repeated this test solely for the 24 transects located within this plant community. In this test, the frequency of *A. diffusa* was again greater at higher sheep density ($B = 0.550$, $SE = 0.09$; $F_{1,22} = 7.04$, $p = 0.014$;).

Table 2. Generalised Linear Models of (A) shrub frequency (mean number per composite 200 m line intercept, per 10-km transect, square-root transformed); (B) shrub height (cm, square-root transformed); both related to sheep density (individuals km^{-2}, square-root transformed). Models have normal error and identity link. Palatability groups consider annual palatability for shrub frequency but spring palatability for shrub height. Within each palatability category (high, medium and low), models control for shrub species ('species') and plant community ('veg', 4 categories); separate models are also shown for the frequency or height of the most abundant shrub species within each palatability category, again controlling for plant community. Strength of support for the effects of sheep density is examined by the ΔAICc on variable removal from that particular model; values in bold represent strong support (ΔAICc > 2.0).

		A) Shrub frequency				**B) Shrub height**			
		df	***B (SE)***	**AICc**	**Δ AICc**	**df**	***B (SE)***	**AICc**	**Δ AICc**
High palatability	**Sheep D**	1	0.125 (0.04)	1193.904	**+6.100**	1	–0.006 (0.005)	734.753	–0.755
	veg	3				3			
	species	6				4			
Alhagi pseudalhagi	**Sheep D**	1	0.443 (0.21)	74.765	–0.703	1	–0.01 (0.01)	56.484	–3.628
	veg	3				3			
Artemisia diffusa	**Sheep D**	1	0.336 (0.1)	274.35	**+4.530**	1	–0.001 (0.003)	68.008	–2.420
	veg	3				3			
Salsola arbuscula	**Sheep D**	1	0.024 (0.05)	224.600	–2.182	1	0.002 (0.007)	228.602	–2.287
	veg	3				3			
Medium palatability	**SheepD**	1	0.085 (0.04)	502.438	+1.304	1	–0.014 (0.005)	342.391	**+4.043**
	veg	3				3			
	species	5				4			
Convolvulus hamadae	**Sheep D**	1	0.210 (0.1)	156.218	+1.215	1	–0.011 (0.004)	76.242	**+4.290**
	veg	3				3			
Astragalus villosissimus	**Sheep D**	1	0.011 (0.06)	166.348	–2.525	1	–0.013 (0.005)	133.925	**+2.566**
	veg	3				3			
Low palatability	**SheepD**	1	0.033 (0.03)	262.150	–1.780	1	–0.008 (0.004)	213.697	+1.084
	veg	3				3			
	species	4				3			

Contrary to expectation, sheep density was not supported as important in models of shrub height for species with high spring palatability (*n* =5) (again, controlling for plant community and individual shrub species; Table 2 B). In contrast, species of medium spring palatability (*n* = 5) were lower on transects with greater sheep density. Unsurprisingly, the height of shrub species of low spring palatability (*n* = 4) was not related to sheep density.

Separate models for the height of the most abundant shrub species within each palatability class confirmed that height was reduced at greater sheep density for two species of medium spring palatability: *Astragalus villosissimus* (Fig.5) and *Convolvulus hamadae* (Table 2 B). Predicted mean height for *A. villosissimus* was 41.6 cm (95% CI; 23.2–65.3) at a density of 20 sheep km^{-2}; 37.3 cm (20.0–60.1) at 40 sheep km^{-2}; and 33.2 cm (16.7–55.3) at 60 sheep km^{-2}, a 20% reduction in height across this range of sheep density (Fig.5). In contrast, no support was found for an effect of sheep density on the height of the abundant, highly palatable *Artemisia diffusa*, *Salsola arbuscula* or *Alhagi pseudalhagi* (in models controlling for plant community). For *Artemisia diffusa* repeating this test solely for those transects located in the *Artemisia*-dominated community again showed no effect of sheep density on *Artemisia* height ($B = 0.049$, 0.09 SE; $F_{1,22} = 2.39$, $p = 0.136$).

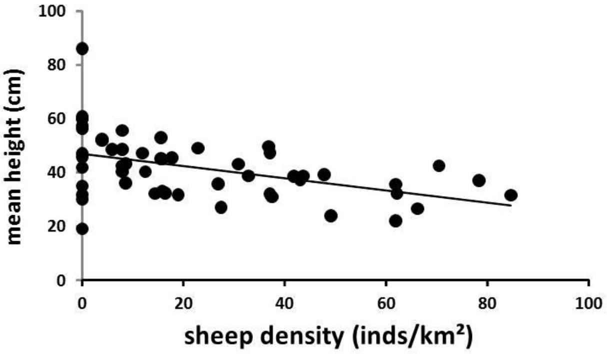

Fig. 5. Mean height (cm) of *Astragalus villosissimus* in relation to transect-specific sheep density (individuals km^{-2}).

Discussion

In the Bukhara study area in 2012 there appeared to be no negative landscape-scale association between livestock density and the abundance and/or distribution of houbara. This is consistent with the lack of a marked effect of livestock on desert shrub vegetation structure and composition, but may mask other potential negative and positive consequences of sheep for houbara. A limitation of our study was the bias towards male observations in both transects and point counts, as found previously for point counts (Le Cuziat et al. 2005b). While females were more likely to be encountered on driven transects than at point counts, the latter provided a more efficient census methodology, with houbara detected at greater distances providing greater numbers of observations and narrower confidence intervals to density estimates.

Our study was designed to examine the effects of sheep grazing on desert shrub structure, density and composition across landscape rather than at local scales. Across the study landscape, extensive areas of rangeland appeared under-utilised, probably due to limitations of water and transport, but elsewhere sheep density ranged from 20–40 individuals km^{-2} (on 2,100 km²) or higher (>40 individuals km^{-2}, on 1,000 km²), locally reaching a maximum of c. 80 individuals km^{-2}. For comparison, in a study of Houbara in Israel, mean sheep densities also reached 80 individuals km^{-2} in parts of houbara breeding area (Lavee 1988). On transects with greater sheep density, we recorded a greater frequency of the most palatable shrubs (controlling for plant community and individual shrub species), suggesting an aggregation of livestock in areas with more food rather than a degradation of habitat from long-term browsing. The palatable *Artemisia diffusa* was more frequent in areas subject to higher livestock pressure. Again, this may be an aggregative response, with pastoralists grazing their sheep on areas that contain more *Artemisia*; nevertheless, given the long-term distribution of grazing determined by proximity to settlements and water, this is evidence that livestock have not denuded these areas. Another possibility is that the higher density is a consequence of pastoralism, as sheep trampling can encourage *Artemisia* regeneration (Gintzburger et al. 2003). No relationship was found between sheep density and the frequency of shrubs of medium or low palatability, indicating that low-palatability shrubs have not increased in density across areas of higher sheep density. Although the height of some shrub species of medium palatability was slightly reduced in the areas supporting greatest densities of sheep, surprisingly sheep browsing did not strongly modify the height of the most palatable shrubs.

Although our results appear to indicate that current patterns of sheep grazing are not degrading desert rangelands within Bukhara, caution is needed. The lack of any difference in height of green shrub growth between areas with low and high stocking density may have been influenced by the wet spring in 2012, which prolonged the growth of ephemeral vegetation, including the palatable *Carex physodes*. In a drier year with less biomass and earlier senescence of ephemeroids, there may be stronger effects of browsing on the annual growth of shrubs. This possibility requires longer-term study.

We found no evidence that houbaras avoided areas with greater densities of livestock. Although our study focused on the distribution of males, and female houbaras may differ in their preference regarding vegetation height (Yang et al. 2002, Yang et al. 2003, Hingrat et al. 2007a), the effects of livestock on habitat structure were found to be subtle, suggesting that a strong response of houbara to habitat quality mediated by livestock is unlikely in our study landscape. This potentially contrasts with the apparent avoidance of areas around wells observed for North African houbara (Le Cuziat et al. 2005a). However, although suggestive, the earlier study did not provide strong evidence that houbara avoided flocks, as incidence and distance to wells may have been confounded with the major effects of topography and distance to agriculture that were not controlled for when examining distance to well (Le Cuziat et al. 2005a). Alternatively, it may be that the intensity of sheep browsing is less in the Kyzylkum. We are unable to compare estimates of sheep density as the study in Morocco quantified this in terms of numbers of sheep flocks while we considered the density of individuals. Nevertheless, pastoralism may differ in other important ways between the regions, for example in rainfall and carrying capacity, the number of camp inhabitants moving with mobile sheep flocks, and the presence of dogs with the flock.

Although we found no strong evidence that browsing of vegetation by sheep modified habitat suitability for male houbara, there may also be other trade-offs relating to livestock. In pastoral areas there is an increased risk of nest trampling by sheep or of predation by dogs, and frequent disturbance by flocks. Shepherds and their dogs may keep female houbara off the nest, potentially leading to failure through overheating of the clutch or predation by avian or ground predators during the period of female absence (Le Cuziat et al. 2005a). On the other hand, shepherds and their flocks may provide protection for houbara nests and broods against predators such as Red Fox *Vulpes vulpes* and Desert Monitor *Varanus griseus* (eaten by shepherds). Nest despoliation by shepherds (Le Cuziat et al. 2005a) or their dogs (Lavee 1988) has been flagged as a problem in other parts of the houbaras' range, but we have no recent evidence of egg collection by shepherds in our study area, and dogs rarely follow flocks but are instead left to guard camps. Subsistence hunting of large ground birds is evidently low in our study area, as firearms are rare and there is some level of state patrol to prevent illegal poaching.

The lack of avoidance by houbaras of areas grazed by livestock is unlikely to be solely a consequence of lek inertia and the site fidelity of individual males (Hingrat et al. 2004), given that the distribution of pastoralism has been fixed for far longer than the generation length of the Asian Houbara (6.6 years for the two houbaras combined: BirdLife International 2012). It is also unlikely to represent an ecological trap, whereby areas appear suitable at the time of settlement but later prove to be suboptimal (Donovan and Thompson 2001), because sheep are brought into the desert at the same time as houbara return to their breeding grounds, so that houbara have the opportunity to settle away from grazed areas. Our observations suggest that houbara are tolerant of sheep and shepherds, skulking or moving away until the disturbance has passed. This is consistent with observations in Spain of Great Bustards (*Otis tarda*), which run away rather than fly when disturbed by sheep flocks, suggesting a lower level of disturbance (Sastre et al. 2009). We have also observed males displaying near regularly used trackways and females nesting in the vicinity of sheep camps. Even so, it could still be argued that the houbara's need for particular habitat structure and topographic features is so important that it will tolerate direct and indirect disturbance from sheep as long as the required habitat features are present.

The findings of this study suggest that the management of houbara stocks and the maintenance of livelihoods in semi-arid lands are not oppositional activities or aspirations. Across the range of the two houbara species it has generally been assumed that livestock overgrazing degrades houbara habitat. That this may not be true, at least in the Kyzylkum Desert, should be a spur to further study in other parts of the species' breeding and wintering range in Central Asia, Arabia and North Africa. Such research will require well-replicated studies conducted at landscape scales.

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References

Alonso, J. C., Alvarez-Martinez, J. M. and Palacin, C. 2012. Leks in ground-displaying birds: hotspots or safe places? - Behavioral Ecology 23: 491-501.

Bailey, T. A., Samour, J. H. and Bailey, T. C. 1998. Hunted by falcons, protected by falconry: Can the houbara bustard (*Chlamydotis undulata macqueenii*) fly into the 21st century? - Journal of Avian Medicine and Surgery 12: 190-201.

Behnke, R. (ed.) 2006. The socio-economic causes and consequences of desertification in Central Asia*,* Springer, Dordrecht.

Behnke, R., Davidson, G., Jabbar, A. and Coughenour, M. 2006. Human and natural factors that influence livestock distributions and rangeland desertification in Turkmenistan. In: Behnke, R. (ed.) The socio-economic causes and consequences of desertification in Central Asia. Springer, Dordrecht, pp. 141-168.

BirdLife International. 2012. Species factsheet: *Chlamydotis undulata*. BirdLife International, Cambridge.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. and Thomas, L. 2001. Introduction to distance sampling: estimating abundance of biological populations*,* Oxford, Oxford University Press.

Carrascal, L. M., Palomino, D., Seoane, J. and Alonso, C. L. 2008. Habitat use and population density of the houbara bustard *Chlamydotis undulata* in Fuerteventura (Canary Islands). - African Journal of Ecology 46: 291-302.

Combreau, O. and Launay, F. 1996. Activity rhythms of houbara bustards (*Chlamydotis undulata macqueenii*) in relation to some abiotic factors. - Journal of Arid Environments 33: 463-472.

Combreau, O., Qiao, J., Lawrence, M., Gao, X., Yao, J., Yang, W. and Launay, F. 2002. Breeding success in a Houbara Bustard *Chlamydotis* [*undulata*] *macqueenii* population on the eastern fringe of the Jungar Basin, People's Republic of China. - Ibis 144: E45-E56.

Coughenour, M., Behnke, R., Lomas, J. and Price, K. 2006. Forage distributions, range condition, and the importance of pastoral movement in Central Asia - a remote sensing study. In: Behnke, R. (ed.) The socio-economic causes and consequences of desertification in Central Asia. Springer, Dordrecht, pp. 45-80.

Donovan, T. M. and Thompson, F. R. 2001. Modeling the ecological trap hypothesis: A habitat and demographic analysis for migrant songbirds. - Ecol Appl 11: 871-882.

FAO. 2006. Livestock's long shadow: Environmental issues and options*,* Rome, Food and Agriculture Organisation.

Freckleton, R. P. 2002. On the misuse of residuals in ecology: regression of residuals versus multiple regression. - Journal of Animal Ecology 71: 542-545.

Gintzburger, G., Toderich, K. N., Mardonov, B. K. and Mahmudov, M. M. 2003. Rangelands of the arid and semi-arid zones in Uzbekistan*,* Paris, CIRAD and ICARDA.

Gubin, B. M. 2004. Drofa-krasotka (Asian Houbara) (in Russian)*,* Almaty Kolor.

Hingrat, Y., St Jalme, M., Ysnel, F., Lacroix, F., Seabury, J. and Rautureau, P. 2004. Relationships between home-range size, sex and season with reference to the mating system of the houbara bustard *Chlamydotis undulata undulata*. - Ibis 146: 314-322.

Hingrat, Y., St Jalme, M., Ysnel, F., Le Nuz, F. and Lacroix, F. 2007a. Habitat use and mating system of the houbara bustard (*Chlamydotis undulata undulata*) in a semidesertic area of North Africa: implications for conservation. - Journal of Ornithology 148: 39-52.

Hingrat, Y., Ysnel, F., Saint Jalme, M., Le Cuziat, J., Beranger, P.-M. and Lacroix, F. 2007b. Assessing habitat and resource availability for an endangered desert bird species in eastern Morocco: the Houbara Bustard. - Biodiversity and Conservation 16: 597-620.

Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weight of birds'eggs. - Auk 96: 73-77.

Ibáñez-Álamo, J.D., Sanllorente, O. and Soler, M. 2012. The impact of researcher disturbance on nest predation rates: a meta-analysis. - Ibis 154: 5-14.

Ibáñez-Álamo, J. D. and Soler, M. 2010. Investigator activities reduce nest predation in blackbirds *Turdus merula*. - Journal of Avian Biology 41: 208-212.

Lavee, D. 1988. Why is the Houbara *Chlamydotis undulata macqueenii* still an endangered species in Israel? - Biological Conservation 45: 47-54.

Le Cuziat, J., Lacroix, F., Roche, P., Vidal, E., Médail, F., N., O. and Béranger, P. M. 2005a. Landscape and human influences on the distribution of the endangered North African houbara bustard (*Chlamydotis undulata undulata*) in Eastern Morocco. - Animal Conservation 8: 143-152.

Le Cuziat, J., Vidal, E., Roche, P. and Lacroix, F. 2005b. Human activities affect the potential distribution of the Houbara Bustard *Chlamydotis undulata undulata*. - Ardeola 52: 21-30.

Lindt, I. 2006. The link between desertification and security in Central Asia. In: Behnke, R. (ed.) The socio-economic causes and consequences of desertification in Central Asia. Springer, Dordrecht, pp. 3-11.

Mallord, J. W., Dolman, P. M., Brown, A. and Sutherland, W. J. 2007. Nest-site characteristics of Woodlarks *Lullula arborea* breeding on heathlands in southern England: are there consequences for nest survival and productivity? - Bird Study 54: 307-314.

Maloney, R. F. 2003. Survival, breeding and movements of reintroduced Asiatic Houbara (*Chlamydotis [undulata] macqueenii*) in Mahazat as-Sayd reserve, Saudi Arabia. University of New England.

Manly, B. F. J., Mcdonlad, L. L., Thomas, D. L., Mcdonald, T. L. and Erickson, W. P. 2002. Resource selection by animals: Statistical design and analysis for field studies. 2nd edition*.,* Dordrecht, Kluwer Academic Publishers.

METI and NASA. 2011. ASTER Global Digital Elevation Model V2. The Ministry of Economy, Trade, and Industry (METI) of Japan and the United States National Aeronautics and Space Administration (NASA)

Military Topographic Directorate. 1985-1991. Soviet General Staff Topographic Maps. Moscow.

Moreira, F. 2004. Distribution patterns and conservation status of four bustard species (Family Otididae) in a montane grassland of South Africa. - Biological Conservation 118: 91-100.

Olson, D. M., Dinerstein, E. D., Wikramanaya, K. E., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P. and Kassem, K. R. 2001. Terrestrial ecoregions of the world: a new map of life on earth. - BioScience 51: 933-938.

Osborne, P. E., Launay, F. and Gliddon, D. 1997. Wintering habitat use by houbara bustards *Chlamydotis undulata* in Abu Dhabi and implications for management. - Biological Conservation 81: 51-56.

Rachkovskaya, E. I. 1995. Vegetation map of Kazakhstan and Middle Asia (Desert Region). Saint Petersburg, Russian Academy of Sciences.

Rich, T., Rebane, M., Fasham, M., Mcmeechan, F. and Dobson, D. 2005. Methods for Surveying Habitats: Ground and shrub vegetation. In: Hill, D., Fasham, M., Tucker, G., Shewry, M. and Shaw, P. (eds.) Handbook of biodiversity methods: Survey, evaluation and monitoring. Cambridge University Press, Cambridge, pp. 201-221.

Riou, S., Judas, J., Lawrence, M., Pole, S. and Combreau, O. 2011. A 10-year assessment of Asian Houbara Bustard populations: trends in Kazakhstan reveal important regional differences. - Bird Conservation International 21: 134-141.

Saint Jalme, M. and van Heezik, Y. 1995. Propagation of the Houbara Bustard*,* London, Keegan Paul International.

Saiz, H. and Alados, C. L. 2012. Changes in semi-arid plant species associations along a livestock grazing gradient. - Plos One 7.

Sastre, P., Ponce, C., Palacin, C., Martin, C. A. and Alonso, J. C. 2009. Disturbances to great bustards (*Otis tarda*) in central Spain: human activities, bird responses and management implications. - European Journal of Wildlife Research 55: 425-432.

Shaumarov, M., Toderich, K. N., Shuyskaya, E. V., Ismail, S., Radjabov, T. F. and Kozan, O. 2012. Participatory management of desert eangelands to improve food security and sustain the natural resource base in Uzbekistan. In: Squires, V. (ed.) Rangeland stewardship in Central Asia: Balancing improved livelihoods, biodiversity conservation and land protection. Springer, Dordrecht, pp. 381-404.

Sheldon, R. D., Kamp, J., Koshkin, M. A., Urazaliev, R. S., Iskakov, T. K., Field, R. H., Salemgareev, A. R., Khrokov, V. V., Zhuly, V. A., Sklyarenko, S. L. and Donald, P. F. 2013. Breeding ecology of the globally threatened Sociable Lapwing *Vanellus gregarius* and the demographic drivers of recent declines. - Journal of Ornithology 154: 501-516.

Silva, J. P., Pinto, M. and Palmeirim, J. M. 2004. Managing landscapes for the little bustard *Tetrax tetrax*: lessons from the study of winter habitat selection. - Biological Conservation 117: 521–528.

SPSS_Inc. 2009. PASW Statistics for Windows. SPSS Inc., Chicago.

Stringer, L. C. 2006. From global environmental discourse to local adaptations and responses: a desertification research agenda for Central Asia. In: Behnke, R. (ed.) The socio-economic causes and consequences of desertification in Central Asia. Springer, Dordrecht, pp. 13-31.

Sutherland, W. J., Pullin, A. S., Dolman, P. M. and Knight, T. M. 2004. The need for evidence-based conservation. - Trends in Ecology and Evolution 19: 305-308.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A. and Burnham, K. P. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. - Journal of Applied Ecology 47: 5-14.

Thompson Iii, F. R., Dijak, W. D. and Burhams, D. E. 1999. Video identification of predators at songbird nests in old fields. - The Auk 116: 259-264.

Tourenq, C., Combreau, O., Lawrence, M., Pole, S. B., Spalton, A., Gao, X. J., Al Baidani, M. and Launay, F. 2005. Alarming houbara bustard population trends in Asia. - Biological Conservation 121: 1-8.

van Heezik, Y. and Seddon, P. J. 1999. Seasonal changes in habitat use by Houbara Bustards *Chlamydotis undulata macqueenii* in northern Saudi Arabia. - Ibis 141: 208-215.

Yang, W.-K., Qiao, J.-F., Combreau, O., Gao, X.-Y. and Zhong, W.-Q. 2003. Breeding habitat selection by the Houbara Bustard *Chlamydotis* [*undulata*] *macqueenii* in Mori, Xinjiang, China. - Zool. Studies 42: 470-475.

Yang, W., Qiao, J., Combreau, O., Gao, X. and Zhong, W. 2002. Display-sites selection by houbara bustard (*Chlamydotis* [*undulata*] *macqueenii*) in Mori, Xinjiang, People's Republic of China. - Journal of Arid Environments 51: 625-631.

Appendix A. Semi-desert shrub species considered in the analysis, showing palatability, and sample sizes (number of individuals measured, % of 10-km transects from which recorded)

Species name	Palatability value	Season	Number measured	% transects
Acanthophyllum borszczowii	low	unpalat	86	27
Aellenia subaphylla	medium	Spr/sum	79	27
Alhagi pseudalhagi	high	Spr/sum	308	17
Ammothamnus lehmannii	low	Wint/aut	48	9
Artemisia diffusa	high	Spr/sum	2167	65
Astragalus villosissimus	medium	Spr/sum	388	56
Calligonum leucocladum	high	Spr/sum	97	33
Calligonum microcarpum	medium	Spr/sum	37	18
Convolvulus divaricatus	low	Spr/sum	199	21
Convolvulus hamadae	medium	Wint/aut	391	44
Haloxylon persicum	high	Spr/sum	92	12
Mausolea eriocarpa	low	unpalat	70	18
Nanophyton erinaceum	medium	Spr/sum	143	13
Peganum harmala	low	unpalat	95	19
Salsola arbuscula	high	Spr/sum	728	80
Salsola gemmascens	high	Wint/aut	386	53
Salsola richteri	medium	Spr/sum	25	8
Salsola rigida	high	Wint/aut	525	59

Chapter 3

Effects of habitat and land use on breeding season density of male Asian Houbara *Chlamydotis macqueenii*

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Abstract

Landscape-scale habitat and land-use influences on Asian Houbara *Chlamydotis macqueenii* (IUCN Vulnerable) remain unstudied, while estimating numbers of this cryptic, low-density, over-hunted species is challenging. In spring 2013, male houbara were recorded at 231 point counts, conducted twice, across a gradient of sheep density and shrub assemblages within 14,300 km² of the Kyzylkum Desert, Uzbekistan. Four sets of models related male abundance to: (1) vegetation structure (shrub height and substrate); (2) shrub assemblage; (3) shrub species composition (multidimensional scaling); (4) remote-sensed derived land-cover (GLOBCOVER, 4 variables). Each set also incorporated measures of landscape rugosity and sheep density. For each set, multi-model inference was applied to generalised linear mixed models of visit-specific counts that included important detectability covariates and point ID as a random effect. Vegetation structure received strongest support, followed by shrub species composition and shrub assemblage, with weakest support for the GLOBCOVER model set. Male houbara numbers were greater with lower mean shrub height, more gravel and flatter surfaces, but were unaffected by sheep density. Male density (mean 0.14 km^{-2}, 95% CI, 0.12–0.15) estimated by distance analysis differed substantially among shrub assemblages, being highest in vegetation dominated by *Salsola rigida* (0.22 [CI, 0.20–0.25]), high in areas of *S. arbuscula* and *Astragalus* (0.14 [CI, 0.13–0.16] and 0.15 [CI, 0.14–0.17] respectively), lower (0.09 [CI, 0.08–0.10]) in *Artemisia* and lowest (0.04 [CI, 0.04–0.05]) in *Calligonum*. The study area was estimated to hold 1,824 males (CI: 1,645–2,030). The spatial distribution of relative male houbara abundance, predicted from vegetation structure models, had the strongest correspondence with observed numbers in both model-calibration and the subsequent year's data. We found no effect of pastoralism on male distribution but potential effects on nesting females are unknown. Density differences among shrub communities suggest extrapolation to estimate country- or range-wide population size must take account of vegetation composition.

Introduction

Sparsely distributed cryptic animals present a serious challenge to researchers. Habitat-suitability modelling allows the relative importance of environmental factors to be assessed and supports distribution and relative density mapping of such species (Peterson 2006; Hirzel and Lay 2008), and this can be used to prioritise areas for management and protection (Renwick et al. 2012; Johnston et al. 2015). However, estimating their actual population size is much more problematic, although this is a necessary requirement for evidence-based management of exploited populations (Waber et al. 2013).

The Asian Houbara *Chlamydotis macqueenii* is a large but cryptic terrestrial bird of sparsely vegetated semi-arid environments stretching from Sinai (Egypt) to Mongolia. Poorly regulated and unsustainable hunting and trapping on both migration routes and wintering grounds (Combreau et al. 2001) have been blamed for declines in Kazakhstan (Tourenq et al. 2004; Tourenq et al. 2005; Riou et al. 2011), which hosts an estimated 77% of the global population (Goriup 1997), resulting in Asian Houbara being listed by the IUCN as Vulnerable (BirdLife International 2015). Habitat degradation from agricultural intensification and overgrazing, combined with human disturbance, is thought also to be affecting the species in parts of its range (Goriup 1997; Combreau et al. 2001; Combreau et al. 2002), albeit with little published evidence.

The conservation response to the plight of the Asian Houbara has focused on large-scale captive-breeding and release (Seddon et al. 1995; Combreau and Smith 1998; Chargé et al. 2014) rather than on improved regulation to render hunting sustainable. However, a further possible measure to part-compensate for the effects of hunting and trapping is the management of local wild populations within the core breeding range. This could take the form of identifying and mitigating region-specific issues affecting habitat quality and extent, local abundance and demography. To establish an evidence base for such management it is necessary (1) to establish the degree to which houbara abundance varies with habitats and with the anthropogenic pressures exerted on them, and (2) to reach a robust estimate of local population size as a benchmark against which to monitor the effects of future interventions.

Several studies have related land-use factors to density and distribution of resident African Houbara *C. undulata* across its range, and indicated that breeding birds are negatively affected by direct and indirect human disturbance, avoiding settlements, major roads, wells, shepherds' camps and agricultural fields (Carrascal et al. 2006; Carrascal et al. 2008; Hingrat et al. 2008; Chammem et al. 2012). In contrast, a study in Iran showed wintering Asian Houbara were associated with croplands (Aghainajafizadeh et al. 2010), while breeding-season distribution of male Asian Houbara was not found to be influenced by pastoralism in Uzbekistan (Koshkin et al. 2014).

Most studies assessing habitat use by wild houbara of both species have operated at the micro-scale: the immediate vicinity of male display sites (10 m x 10 m, Yang et al. 2002b), nests (10 m x 10 m, in both Yang et al. 2002b; Aghanajafizadeh et al. 2012), tracks (2.5 m width, Launay et al. 1997b) or telemetry locations (50 m x 3 m, Combreau and Smith 1997; 100 m radius, Hingrat et al. 2007). However, heterogeneity of topography, vegetation and soil, and a need for conservation planning on a regional extent necessitates the study of how density varies at landscape rather than micro-site scales. Other studies have examined the influence of habitat and land-use characteristics on houbara presence/absence at larger spatial scales, i.e. for 500 m walked transects (Carrascal et al. 2008) or 20 km x 20 km grid cells (Chammem et al. 2012). Van Heezik and Seddon (1999) examined Asian Houbara habitat selection among seven habitats (defined by landform and substrate) in Saudi Arabia, using a sample of sightings (n = 229) collected along standardised drives within a study area of about 750 km^2, and found that probability of selection for different habitats varied with season. However, sex was not considered and analysis of habitat selection was performed on observation data merged across four years to obtain sufficient sample sizes.

Density estimates are necessary for the extrapolation of population sizes, which can then potentially be used to inform sustainable harvest quotas and in the assessment of conservation status. However, few recent estimates exist for migrant houbara population sizes in the breeding range from Central Asia to Mongolia. In the mid-1990s the global population of the Asian Houbara was estimated at 39,000 – 52,000 individuals, of which 77% were in Kazakhstan and 15% in Uzbekistan (Goriup 1997). This estimate, however, extrapolated country-wide numbers from local estimates (Gubin 1992; Mitropolsky et al. 1996). Subsequent studies that provided density estimates for several subpopulations in Kazakhstan (Tourenq et al. 2004; Tourenq et al. 2005; Riou et al. 2011) experienced methodological limitations (see Discussion), while for Uzbekistan the two assessments available were considered preliminary and provisional (Launay et al. 1997a; Koshkin et al. 2014).

To our knowledge, no previous study has sought to establish regional population sizes by comparing houbara breeding densities among habitats at the landscape scale. Here we assess the effects of habitat and human land-use on houbara abundance and provide the first robust estimate of density and a regional population size for this species.

Methods

Study area

The study area (39.34–40.56°N 62.21–65.20°E, 170–400 m above sea level; approximately 14,300 km²) is located in the Bukhara District of Uzbekistan, within the Kyzylkum part of the Southern Central Asian Desert (Fig.1). The terrain is predominantly flat to gently rolling, bounded to the north and east by low dry mountains, and to the south-east by irrigated croplands and permanent settlements. Plant communities are dominated by drought-resistant and halophytic shrubs, with shrub assemblage and vegetation structure varying with landform and substrate (gypseous soils, consolidated or loose sands), resulting in a mosaic of habitats at the landscape scale. Although largely unpopulated with only a few scattered small settlements, parts of the area are grazed in spring by mixed flocks of sheep (predominantly) and goats (hereafter 'sheep'). Most such livestock is managed from seasonal camps and their distribution is limited by the distribution of functioning wells and to areas to which water can be transported. Thus livestock densities are highest in areas closer to settlements and permanent water sources leaving substantial areas of the desert sheep- free (Koshkin et al. 2014).

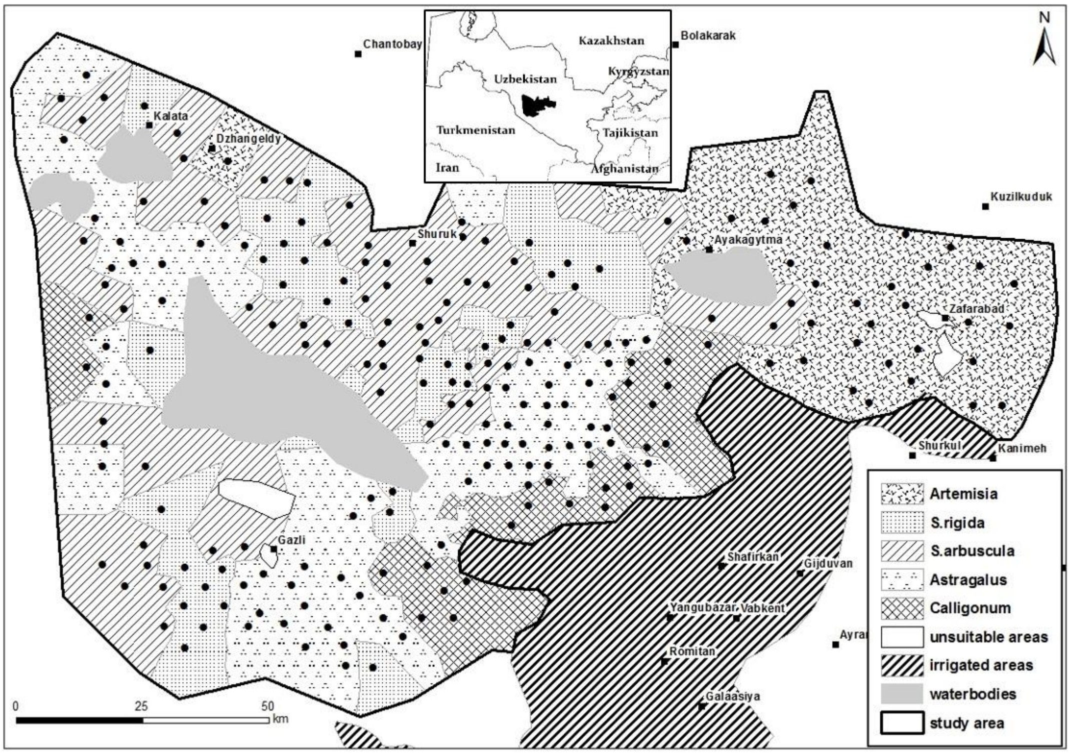

Fig. 1 Study area within Bukhara District of Uzbekistan, Southern Kyzylkum Desert, showing point count locations (black dots) in relation to five shrub assemblages classified during this study

Sampling of houbara

Houbara are shy and difficult to see. However, during the breeding season (March – May) displaying males (and also floating males; see SOM, section 4) are conspicuous and can be apparent from long distances. This provides an opportunity for male population assessment with a relatively high degree of accuracy. From 24 March to 19 May 2013, two counts several weeks apart were made at each of 231 points across the study area. Counts were repeated at each location to reduce sampling error from weather or time of day. Subsequent analyses of visit-specific counts allowed these factors, as well as season (detectability was expected to decrease as the season progressed) to be controlled for in analyses of abundance; while separate analysis of the maximum count across two visits did not account for these covariates. Point count locations were randomly selected (excluding known unsuitable breeding habitats e.g. wetlands, mountains, irrigated and built-up areas), originally stratifying sampling effort across four shrub assemblages as mapped by Rachovskaya (1995): *Artemisia*, *Salsola* spp., *Astragalus* and *Calligonum*, following Koshkin et al. (2014). Locations were a minimum of 4 km apart to avoid pseudo-replication and reduce spatial autocorrelation. The classification and distribution of shrub assemblages was subsequently refined using vegetation data collected during this study, providing the following revised distribution of sampling locations: *Artemisia* (2,873 km^2), *n* = 33; *Salsola arbuscula* (3,904 km^2), *n* = 67; *S. rigida* (2,180 km^2), *n* = 36; *Astragalus* (3,778 km^2), *n* = 69; and *Calligonum* (1,603 km^2), *n* = 26 (Fig.1). For a full description of vegetation sampling, classification and assemblages see (SOM, section 1).

Each count was conducted from the most appropriate vantage point (highest point, typically a small rise) within 400 m of the location originally selected in GIS, with the second count conducted from the same point. Each point count (an initial scan with binoculars followed by extensive scanning with a 20–60x telescope) lasted 30 minutes and was undertaken by a single observer during the period of peak male display activity (i.e. within three hours after sunrise and two hours before sunset; (Combreau and Launay 1996)). For each houbara or houbara group observed, the sex, age, number of individuals, distance from observer (measured by laser rangefinder up to 1,400 m) and activity (flying, walking, standing, crouching and/or displaying) and time of observation were recorded. Combination of plumage and structure of head and neck, as well as relative size of individuals in a group was used to sex non-displaying birds. Observations beyond 1,400 m could not be reliably measured by rangefinder and were therefore excluded from further analysis to avoid error and potential bias in density estimation (Buckland et al. 2001). As weather conditions may affect behaviour and thus detectability, wind strength was recorded during each point count (0 = no wind, 3 = strong wind; see Table 1). Other conditions, such as fog and morning dew, which could affect bird's behaviour and visibility were not encountered during the study, whereas counts were not conducted during rain.

Table 1 Candidate environmental and landscape context variables for models of male Asian Houbara abundance

Variable name	Description	Type of data
Detectability variables		
date	Date on which a count was conducted, first day = 24 March	continuous
visit	First or second visit to a point count	categorical
time categorical	Time of the count (1 = morning, 2 = afternoon)	categorical
time continuous	Time of the count (minutes after sunrise/before sunset)	continuous
$time^2$	Time of the count (squared)	categorical
$time^3$	Time of the count (cubed)	categorical
wind	Estimated wind strength during point count/Beaufort scale equivalent (1/0 = no wind, 2/1-2 = weak, 3/3-4 = medium, 4/5-6 = strong)	categorical
shrub height	Mean height of all shrubs (cm) (n = 28 species, excluding the very short *Salsola gemmascens* and *Nanophyton erinaceum* (mean <12 cm), pooled per point count)	continuous
Land-use variables		
sheep density	Mean density (individuals km^{-2}) extracted from 2 km radius buffers around point count location	continuous
Habitat variables		
shrub height	as above	continuous
substrate PCA1	Sample score from first axis of unrotated principal component analysis (PCA) performed in PRIMER 6.1.10 on correlation matrix of unconsolidated sand, consolidated sand, gravel and clay cover	continuous
substrate PCA2	Sample score from second PCA axis	continuous
shrub MDS1	Sample score of multidimensional scaling (MDS) ordination of the covariance matrix of composite shrub frequency data (4 x 50 m line intercepts) from each of 817 locations (2012-2014 data), performed in PRIMER 6.1.10	continuous
shrub MDS2	Sample score from second MDS axis	continuous
DEM SD	Landscape rugosity - standard deviation values of elevation (m), extracted from 2 km buffers around point counts (ASTER GDEM V2, horizontal resolution 30 m, vertical resolution one meter)	continuous
shrub assemblage	Sample locations overlaid on mapped distribution of five shrub assemblages, classified by cluster analysis of shrub frequency at 817 locations (2012-2014 data)	categorical
GLOBCOVER	The proportion of grid squares from three aggregate global land-cover (GLC2000, approx. 700 m x 900 m spatial resolution) classes within two km buffers around point count locations: *Globcover: vegetation* (highest % grids classified as herbaceous and shrub cover); *Globcover: consol.* (highest % of consolidated sand); *Globcover: unconsol* (highest % of unconsolidated sand) and *Globcover: diversity* (Simpson's Diversity Index, adjusted to equitability).	categorical

Detectability covariates and estimates of male houbara density and numbers

Five *a priori* factors, *date*, *visit*, *time*, *wind*, *shrub height* and landscape rugosity (a measure of terrain unevenness; *DEM SD*), were postulated to affect houbara detectability (see Table 1). The first four may influence the incidence of male display, while shrub height and landscape rugosity could influence visibility (SOM, section 2). Their effects on detectability were examined in a series of multiple-covariate distance sampling (MCDS) models within DISTANCE 6.0, which also examined alternative continuous, quadratic or categorical formulations (SOM, section 2). Those detectability covariates supported by the best MCDS model (lowest AIC) were subsequently included in distance models used to estimate houbara density and population size and in subsequent multivariate species-habitat models.

The density of male houbara in each of the five shrub assemblages was estimated by MCDS models that incorporated supported detectability variables, stratifying encounter rate and density by shrub assemblage, and the total number of males was estimated as the area-weighted mean of assemblage-specific estimates.

Habitat and land-use variables

To examine the potential influence of habitat, landform and land-use on houbara abundance, six habitat variables (landscape rugosity, remote sensed land-cover, and field derived measures of soil [substrate] type, shrub vegetation composition and structure) and one anthropogenic variable (sheep density) were considered (Table 1). The mean seasonal sheep density around each point was extracted from an interpolated density surface based on multiple distance transects, rather than visit-specific measures that would be affected by sampling error relative to daily flock movements. Field measures of substrate, shrub composition, assemblage class and structure taken around each point-count were used in model calibration. Similar measures were taken at an additional 586 sampling locations across the study area, allowing interpolation to calculate assemblage extent (for habitat-area weighted population estimates) and resampling when predicting abundance using multivariate habitat models.

Shrub species composition and structure measurements were taken along four 50 m line intercepts located 500 m from each of the 231 point count locations during 16 May–6 June 2013, and from an additional 586 locations sampled during May–June 2012, 2013 and 2014 (for details on sampling, please see SOM, section 1). Pooled line intercept data were used to calculate average *shrub height* (considered as a measure of concealment and potentially also the availability of invertebrate prey). Substrate cover i.e. clay, consolidated sand, drifting sand and gravel was measured in one 2 m x 2m quadrat per line intercept and pooled means were reduced to two orthogonal variables, *substrate PCA1* and *substrate PCA2* (Table 1), by unrotated Principal Component Analysis performed on the correlation matrix in PRIMER 6.1.10. Shrub species were identified following Gintzburger et al. (2003); further sampling details are provided in 'Supplementary materials' (SOM, section 1). Shrub composition was considered separately in terms of classification of five categorical *shrub assemblage* (by cluster analysis, SOM, section 1), or as two uncorrelated ordination axes obtained by multidimensional scaling (MDS): *shrub MDS1* and *shrub MDS2* (SOM, Fig.S1). Shrub assemblage, shrub structure and substrate were interpolated (using Inverse Distance Weighted tool in ArcMap 10.1) across the study area from data recorded at all 817 sampling locations. As the habitat and landscape-context selected by the most distant birds affect numbers seen within 1.4 km of a point count, sheep density, rugosity and land-cover were extracted from a buffer of 2 km around the point.

To test if freely available remotely sensed land-cover classification provided meaningful models of abundance, thus removing the need for detailed field measures, we used global land-cover data (GLC 2000) (Bartholomé and Belward 2005), with proportionate cover of each of three aggregate classes (see Table 1 for definitions) extracted within a 2 km buffer around points using ArcMap 10.1. Land-cover diversity within each buffer was calculated as Simpson's Diversity Index, D (Simpson 1949), adjusted to equitability (evenness), E_D following:

$$E_D = \frac{D}{D_{max}} = \frac{1}{S\sum_{i=1}^{3} p_i^2}$$

where D_{max} is the maximum value D could assume if the three land-cover classes were evenly distributed and p_i the proportion of the ith class.

Landscape rugosity (*DEM SD*) was obtained from ASTER GDEM V2 (NASA 2011), with low and high *DEM SD* values indicating flat and undulating/dissected terrain respectively.

Sheep were counted along a total of 947 five-kilometre transects between 26 March and 31 May 2013 from a vehicle driven at 30–50 km/h along trackways, with a minimum of 2 km between consecutive transects to avoid spatio-temporal autocorrelation. Sheep are walked across the desert all day excluding sunrise and sunset, when they are herded to or from camps; so counts were conducted between 08:00–17:00. For each flock, numbers were counted (using binoculars) and the perpendicular distance to the flock centre, following Buckland et al. (2001), measured by rangefinder. Sheep density was estimated by distance analysis and an interpolated surface was created (SOM, section 3).

Multivariate models of houbara distribution

Habitat, land-cover, landform and land-use effects on visit-specific counts of male houbara were examined by random intercept Generalised Linear Mixed Models (GLMMs) with Poisson error, constructed in R (lme4 package), allowing detectability covariates supported by distance analysis to be incorporated as fixed effects and including point identity (ID) as a random effect to control for repeat visits. However, to extrapolate relative abundance across the study area we also constructed separate Generalised Linear Models (GLMs) of maximum count across the two visits (as the random effect of point ID cannot be extrapolated for unsampled areas). Binomial mixture models were considered inappropriate as their assumption of a static population between resampling events (Royle 2004) was probably violated (SOM, section 4). Strong intercorrelation, defined as r >0.5, following Freckleton (2002), was found between *shrub MDS1* and *substrate PCA1* (r = -0.645) and between *shrub MDS1* and *shrub height* (r = -0.580). Therefore, physical vegetation and substrate measures were considered separately from shrub composition data for analysis, resulting in four sets of environmental models: (1) 'Vegetation structure': *shrub height* + *substrate PCA1* + *substrate PCA2*; (2) 'Shrub assemblage': *shrub assemblage*; (3) 'Shrub MDS': *shrub MDS1* + *shrub MDS2*; (4) '*GLOBCOVER'* (four continuous variables). All environmental models also considered the effect of landscape rugosity and sheep density.

For model selection multi-model inference (MMI) in an information theoretic framework was applied to each of the four sets of candidate models, following Burnham and Anderson (2002), using the 'MuMIn' package in R (Barton 2013). Model-averaged parameter estimates, their unconditional errors and the relative support for each variable (Relative Variable Importance, RVI, scale 0–1) were calculated across the

95% model confidence set. However, variables which have no effect accumulate weight through their presence in models that gain support by their inclusion of important variables. Therefore, to assess the relative importance of candidate predictors we examined the 95% interval of RVI distribution of a simulated random *null variable* (mean = 1, *SD* = 1) iterated across 1,000 MMI iterations, following Boughey et al. (2011). Candidate variables with an RVI beyond the 95% *null* distribution and with a model average coefficient 95% confidence limit (calculated from unconditional standard errors) not spanning zero were considered to have support (following Boughey et al. 2011). All models were run in R 3.0.2 (R Core Team 2013). Potential spatial autocorrelation in model-averaged residuals was examined by Moran's I in R (Graf et al. 2005).

The mapped relative distribution predicted by MMI species-habitat models was examined by overlaying a grid (resolution 1,836 m x 1,836 m, cell area = 3.371 km^2) on the study area, providing a grid cell area equal to that encompassed by the estimated effective detection radius (EDR; 1,036 m) around point counts (see results). Values of each variable were extracted from each cell and numbers were predicted from the model-averaged 95% confidence subset of candidate GLM models for each model set. Temporal transferability of models was examined by repeating surveys twice at 140 of the points in 2014 and inspecting the correlation (R^2) between predicted (abundance values extracted from grid cells intersecting point count location) and observed (maximum number of birds per point count) abundance.

Results

During 2013, at point count locations (n = 231) 317 individuals or small groups of houbara were recorded, comprising 321 adults and 15 juveniles. Of the adults that could be sexed (*n* = 311, 98%) 94% were males; females were substantially under-recorded as they are far more cryptic than males in the breeding season, with many incubating during the survey period (Burnside, unpublished data). Observations of females were therefore excluded and unsexed birds and males were pooled for subsequent analysis, adjusting for the estimated proportion of males among unsexed birds in density estimates.

Habitat gradients

A total of 65,939 shrubs were identified and measured along 155.1 km of walked line intercepts at 817 sampling locations (mean of 46.8 shrubs per composite sample, *SD* = 34.2, range 0–233 shrubs). Mean shrub height varied from over 45 cm in the west and south, mainly in *Astragalus* and *Calligonum*, to under 30 cm in *Artemisia*, *Salsola rigida* and *S. arbuscula* assemblages (SOM, Fig.S2d).

The first substrate component (*Substrate PC1*) explained 59.2% of the variance and represented a gradient from greater cover of clay to greater cover of consolidated sand; gravel and drifting sand had negligible loadings on this component. The second component (*Substrate PC2*) explained a further 20.4% of the variance, with a gradient from gravel (low values) to drifting sand (high values) (SOM, Fig.S3). Dominant substrate types differed between shrub assemblages, with >50% cover of clay in both *Artemisia* and *Salsola rigida*, >75% cover of consolidated sand in *Astragalus* and the highest cover of drifting sand (18%) in *Calligonum* (SOM, Fig.S4).

Sheep density differed among shrub assemblages ($F_{4,761} = 32.5$, $p = 0.001$, all pair-wise Tukey $p < 0.05$), being highest in *Calligonum* (mean 40.0 individuals km^{-2} ± 2.1[*SE*]), similar between *Astragalus* and *Artemisia* (31.5 ± 1.5; 24.7 ± 2.2, Tukey $p > 0.05$) and lowest in *Salsola arbuscula* (19.4 ± 1.3) and *S. rigida* (14.4 ± 1.5) (SOM Fig.S2a), but variation within shrub assemblages was high and overall variance explained by shrub assemblage was low (GLM, $R^2 = 0.17$), allowing independent effects to be tested.

Detectability covariates and estimates of male houbara density

In distance analysis of houbara observations, half-normal functions with cosine adjustments provided the best fit, with a mean EDR of 1,036 m (95% confidence interval [CI]; 985 – 1,091). A 400 m-wide trough in radial distance suggests that some houbara near to the observers either crouched and remained undetected, or (more likely) sneaked off and were subsequently detected when over 400 m away (Fig.2). The best MCDS model included *visit* (season effect) and *time categorical* (am/pm) covariates, which improved model fit (ΔAICc = -5.6) relative to a null model. The three closest competing MCDS models also included combinations of both season (*visit* or *date*) and time of day (*time categorical*, or *time* + *time*^{2}) and provided similar density estimates and

CIs; these represent alternative formulation of the same detectability effects (SOM, Table S1,A). Therefore *visit* and *time categorical* were included in subsequent distance models of houbara density and as fixed effects in all multivariate abundance-habitat models. Three models that also incorporated *shrub height* and *wind* were within two AICc units of the best model but addition of these covariates to the best model did not improve model fit or alter the detection function (maximum EDR change 1 m) or density estimate (SOM, Table S1,B); thus there is no evidence that they affected detectability. As shrub height did not affect detectability it was included as a candidate variable in subsequent multivariate models of habitat association.

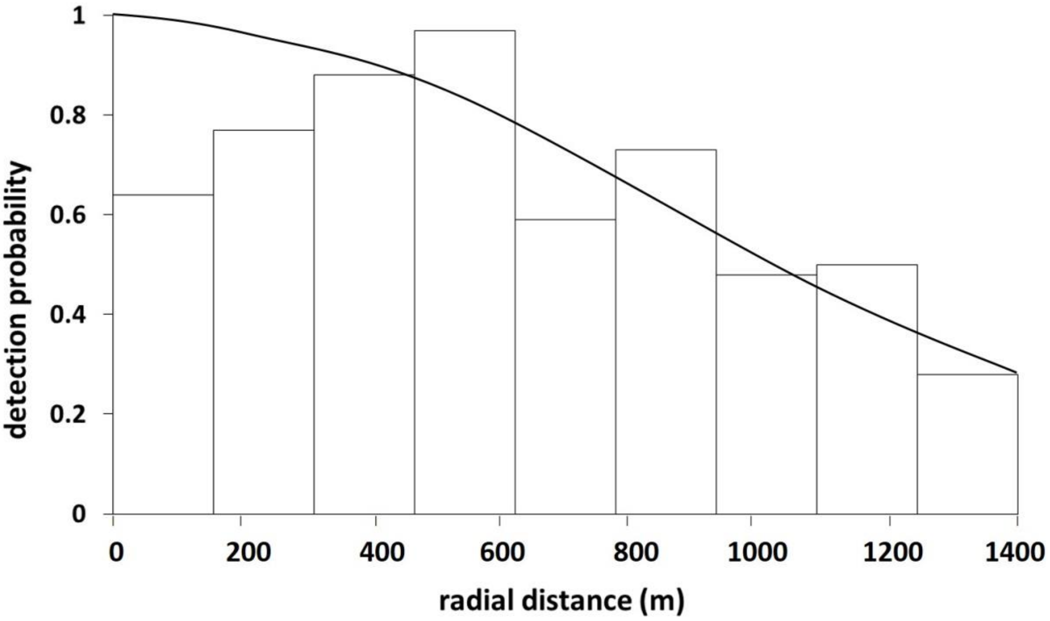

Fig. 2 Probability of detection of male houbara on point counts, based on the best MCDS model (including *visit* and *time categorical* as detectability covariates), with half-normal detection function (with cosine adjustment) fitted to visit-specific count data, truncated at 1,400 m distance from the observer.

Inclusion of detectability covariates improved model fit and marginally increased precision (Table 2). In 2013, mean male density across the study area was 0.14 km^{-2} (95% CI; 0.12–0.15; unstratified MCDS model). Stratified by shrub assemblage, density was highest in *S. rigida* (0.22 males km^{-2} [95% CI; 0.20–0.25]); lower but similar between *Astragalus* and *S. arbuscula* (0.15 [0.14–0.17] and 0.14 [0.13–0.16]); lower again in *Artemisia* (0.09 [0.08–0.10]); and lowest in *Calligonum* (0.04 [0.04–0.05]). The total number of males was similar when estimated with (1,824 [95% CI; 1,645–2,030]) and without (1,886 [95% CI; 1,698–2,089]) stratification by shrub assemblage, as sampling intensity was largely proportionate to assemblage extent.

Table 2 Comparison of density and population estimates of male Asian Houbara on point counts (including observations of unsexed birds and adjusting for proportion of males among sexed) from conventional distance sampling (CDS) models (not including detectability covariates) and alternate unstratified and stratified multi-covariate distance sampling (MCDS) models that included *visit* and *time categorical* detectability covariates. For all models observations were truncated at 1.4 km distance.

Model (strata)	AICc	Goodness of fit (Cramer von Mises)	Density estimate (birds/km², 95% CI)	Total population estimate (birds, 95% CI)
CDS (null model)	3109.3	0.0798	0.135 (0.111– 0.164)	
MSDC	3103.7	0.0618	0.140 (0.126 – 0.155)	1,886 (1,698 – 2,089)
MSDC (5 Strata)	3103.7	0.0618		1,824 (1,645 – 2,030)
Artemisia			0.090 (0.081 – 0.100)	243 (218 – 270)
Astragalus			0.150 (0.136 – 0.167)	532 (483 – 594)
Calligonum			0.041 (0.037 – 0.046)	61 (55 – 69)
Salsola arbuscula			0.146 (0.131 – 0.162)	529 (477 – 588)
Salsola rigida			0.223 (0.200 – 0.248)	457 (410 – 509)

Houbara habitat and land-use associations

Residuals of model-averaged GLM and GLMM models were not spatially auto-correlated for all four model sets (all Moran's I <0.01).

In MMI of the 'Vegetation structure' model set, effects of *shrub height*, *substrate PCA2* and *DEM SD* were all strongly supported (Fig.3a), with greater numbers of males in areas with perennial shrubs of lower height, less cover of drifting sand relative to gravel and in flatter areas. The 'Shrub assemblage' MMI showed strong support only for effects of *shrub assemblage* (Fig.3b), suggesting male numbers were highest in *S. rigida*, lower in *Artemisia*, *Astragalus* and *S. arbuscula* and lowest in *Calligonum* (see Fig.3 text for parameter estimates), consistent with results from stratified MCDS (Table 2). The 'Shrub MDS' MMI showed support for both *shrub MDS1* and *shrub MDS2*, but the positive loading on MDS1 of both preferred (*Astragalus*) and less preferred (*Calligonum*) shrub species (SOM, Fig.S1) makes interpretation problematic (Fig.3c). No candidate variables were supported within the 'GLOBCOVER' model set, with all RVIs within the 95% null interval and CIs spanning zero (Fig.3d), precluding its use in spatial extrapolation. Irrespective of the vegetation classification used there was no support for any effect of *sheep density* on male houbara density.

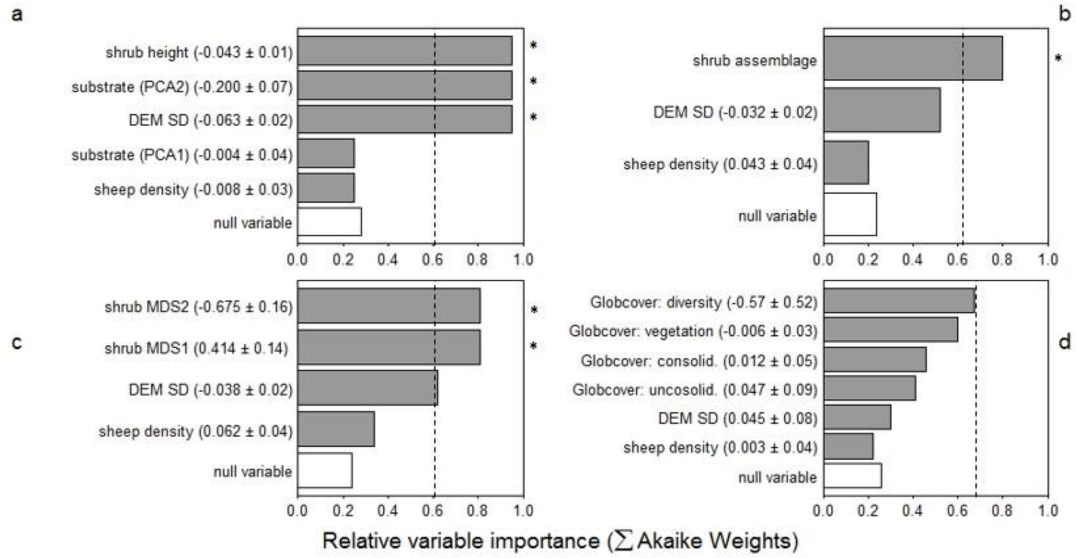

Fig. 3 Relative variable importance (RVI) and model averaged coefficients ± SE for each predictor, calculated across each of four 95% confidence sets of candidate generalised linear mixed models (GLMM) considering (a) Vegetation structure; b) Shrub assemblage (five categories: *S. rigida* [mean coefficient 0.528 ± 0.31 SE], *S. arbuscula* [-0.166± 0.29], *Calligonum* [-0.906 ± 0.43], *Astragalus* [0.094 ± 0.31], referenced to *Artemisia*); c) Shrub MDS; (d) GLOBCOVER. All models also included point ID as a random effect and visit (first or second) and time (morning or evening) as fixed effects (RVI = 1, not shown). See Table 1 for definition of predictors. Unfilled bars and the vertical dashed line show the median and 95% limit of RVI of a random null variable (across 1,000 MMI iterations); * denotes strongly supported predictors.

Abundance estimates

Relative abundance mapped and extrapolated from the 'Vegetation structure' GLM model set had the strongest correspondence with calibration data from both 2013 and 2014 (R^2 = 0.22 and 0.15 respectively) (Fig.4), with weak negative relation between observed and predicted data for 'Shrub assemblage' (R^2 = 0.01, 0.006) and 'Shrub MDS' model sets (R^2 = 0.04, 0.08) (SOM, Fig.S5).

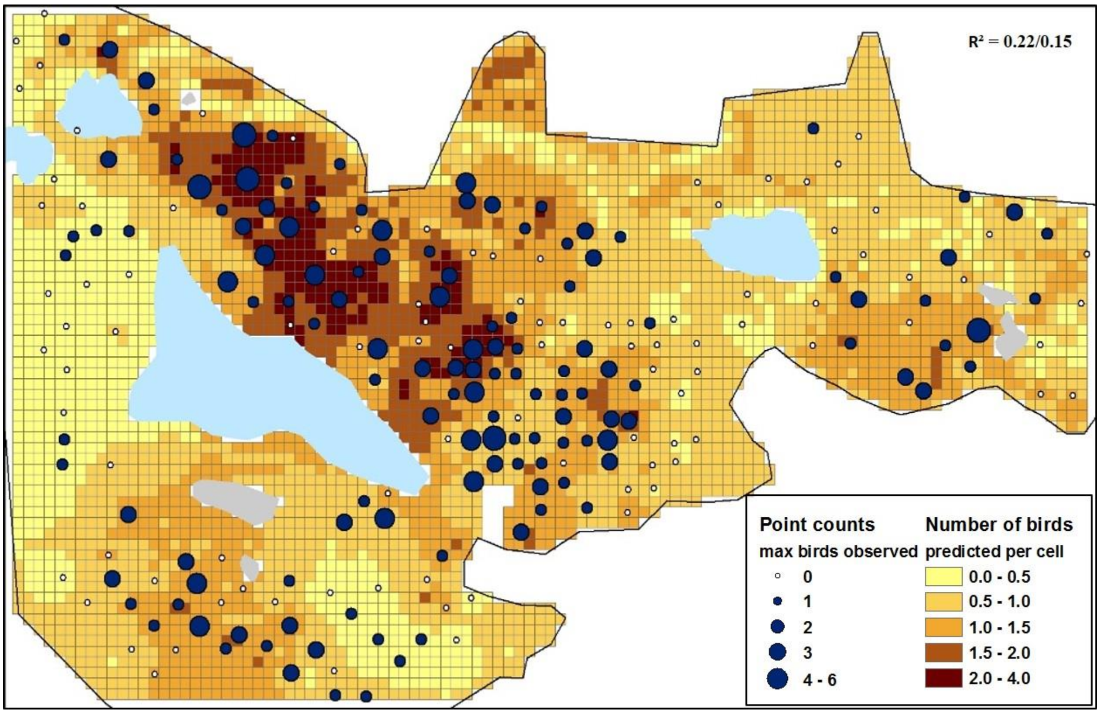

Fig. 4 Distribution of male Asian Houbara density across the Bukhara District in Uzbekistan predicted from the averaged 'Vegetation structure' MMI model set, overlaid with the observed maximum numbers seen during point counts in 2013. R^2 indicates correspondence of predicted abundance with observed point count maxima in the model calibration year (2013) and subsequent year (2014).

Discussion

Within the southern Kyzylkum Desert, the abundance of male houbara during the breeding season is higher in areas of flatter terrain with shorter shrub vegetation, characteristic of areas with more gravel, factors all probably consistent with display visibility. Male houbara occurred at highest density in areas characterised by *Salsola rigida*, intermediate densities in *Astragalus* or *S. arbuscula* and at lower density in *Calligonum*, but shrub structure was a better predictor of abundance than shrub composition. Sheep density did not affect the abundance of male houbara within the study area.

Habitat effects

The increasing prevalence of males in shorter vegetation and flatter terrain may have several explanations, not necessarily mutually exclusive. Probably most important are the need to be visible to females and to have enough open ground in which to conduct their display which involves a fast run, sometimes for long distances (Gaucher et al. 1996). Apparent selection for gravel is likely a consequence of the sparse short-statured shrub vegetation in such areas. Moreover, an unhindered view of the surrounding terrain allows the detection of both predators and approaching/passing females, but it is also possible that flat terrain also reduces the locomotion cost for these large cursorial birds. The combination of medium to short shrubs and flat terrain seems to be the most favourable habitat for male houbara in the study area.

The probability of occurrence of African houbara in flat terrain (areas with slope of the terrain <15%) has been reported for a breeding population in Lanzarote, Canary Islands (Carrascal et al. 2006). However, this is the first study to show how vertical vegetation structure can influence houbara numbers at landscape-scales. With the exception of Carrascal et al. (2008), other studies have not considered shrub height, possibly due to huge effort needed to robustly collect such data (van Heezik and Seddon 1999; Yang et al. 2002a; Hingrat et al. 2008; Chammem et al. 2012). The study by Carrascal et al. (2008) did not find an influence of shrub height, however, this compared mean shrub height at presence versus absence sites across a range of suitable and unsuitable habitats, dominated by short vegetation and therefore other features, such as sandy substrate, were more influential at this scale of analysis. Studies that assessed houbara habitat use without sex differentiation, through sampling tracks or telemetry locations (Combreau and Smith 1997; Launay et al. 1997b), are not comparable to ours as habitat use is expected to differ between males and females (Hingrat et al. 2007).

Male houbara densities differed among the five shrub assemblages. Sparse short halophytic vegetation dominated by *Salsola rigida* supported the highest density (Table 2). Lower densities (similar to each other) occurred in vegetation dominated by *Astragalus villosissimus* and *Salsola arbuscula*. Owing to the large area they occupy (= 7,682 km²), the latter two assemblages together hold over 50% of all males estimated for the Bukhara study area. *Calligonum* and *Artemisia* shrub assemblages supported lower densities of male houbara. *Calligonum* comprises a rich diversity of shrubs on drifting sand, including *Calligonum* sp., *Convolvulus* sp. and *Astragalus villosissimus*. The main limiting factor for male houbara here is most likely the mean height of vegetation (>0.5 m), which presumably impairs visibility of their display. *Artemisia* shrub assemblages (dominated by *A. diffusa*) prevail in the most elevated parts of the study area but although plants of this genus are palatable to houbara (Gubin 2004) they are not thought to be preferred food during the breeding season (J. Al-Khaili pers. comm.).

Also, owing to the uniform low height and hence poor concealment by the vegetation, these areas might be less suitable for nesting females. If the houbara 'exploded lek' system follows a 'hotspot' model (Beehler and Foster 1988) (i.e. males lek where females congregate for resources), it is possible that lower suitability of both *Calligonum* and *Artemisia* assemblages for breeding females may affect male densities. Both MDS predictors were supported, indicating that density of male houbara was affected by shrub species composition, but neither shrub assemblage nor MDS gave as good an explanation of male distribution as shrub structure. This suggests males primarily respond to shrub structure, for which composition is a proxy, rather than to systematic differences in resource availability among shrub assemblages.

Land-use effects

Our evidence that, at landscape scales, male houbara do not avoid areas with greater sheep densities (highest mean per point count >100 individuals km^{-2}) confirms an earlier study (Koshkin et al. 2014) and agrees with findings on African Houbara in Tunisia (Chammem et al. 2012) but not from Morocco (Le Cuziat et al. 2005a; 2005b). The discrepancy with Morocco perhaps reflects differences between rangeland systems. In Morocco (Le Cuziat et al. 2005b) and in Tunisia (Combreau, personal communication), sheep and goats grazed desert adjacent to wells all year round, thus permanently affecting vegetation, whereas in the more strongly seasonal pastoralism of Uzbekistan grazing is predominantly confined to the spring and early summer months. Such seasonal pastoralism, which is probably the most important and widespread land-use within the entire range of the Asian Houbara, appears to have no negative impact on either *Chlamydotis* species or their habitat (Gamoun 2014; Koshkin et al. 2014), at least at the range of sheep densities examined. However, caution is needed on this issue, as disturbance of nesting females and incidental nest destruction by livestock and egg-taking by shepherds, together suggested to be the main threats for a population in Israel (Lavee 1988), cannot be discounted.

Houbara population estimate

Our estimate of 0.14 male houbara km^{-2} (95% CI; 0.12–0.15) suggests 0.28 (0.24–0.30) adult houbara overall for the study area in Uzbekistan, if an equal sex ratio can be assumed (following Combreau et al. 2002). However, comparison with densities estimated for other Asian Houbara populations is problematic. Most recent studies used driven transects (Tourenq et al. 2004; Tourenq et al. 2005; Gubin 2008; Riou et al. 2011) and each had methodological drawbacks. In Koshkin et al. (2014) point counts were found to perform better than transects, at least in the conditions of the southern Kyzylkum. Gubin (2008) based multi-annual estimates for several areas in south-western Kazakhstan on numbers of individuals recorded along driven transects within a 200 m survey strip (range of 0.01–0.24 birds/km^2); this may indicate relative abundance among areas, but as detectability was unknown it is not possible to account for undetected birds to estimate density. Although Riou et al. (2011) and Tourenq et al. (2004; 2005) used distance analysis, distance measurements were not taken and the effective strip width (ESW) is not reported, analysis pooled across regions with differing relative abundance resulting in wide uncertainty, and timing and sex composition are not reported. Although more females are detected during driven transects (30% of adult birds) than on point counts (7%) (Koshkin et al. 2014) densities estimated by Riou et al. (2011) and Tourenq et al. (2004; 2005) will have been underestimated to an unknown extent. Depending on timing, estimates may lie somewhere between an estimate of male numbers (comparable to our male estimate) for survey during incubation (when females are infrequently observed even on driven transects) to an estimate comprising both males and females during brood-rearing/post-nesting, closer to, but still likely underestimating total numbers.

With these considerations, our estimate of male houbara density appears substantially greater than breeding densities observed in Oman (average across three years, 0.03 birds km^{-2} [inter-annual range 0.01–0.05 birds km^{-2}]) (Tourenq et al. 2005) and in three regions of Kazakhstan, each averaged across three 3-year periods (Riou et al. 2011): 'Kyzylkum', 0.05 birds km^{-2} (inter-period range 0.04–0.06); 'Karakum', 0.02 (0.01–0.02) and 'North east' 0.01 (0.008–0.02); but comparable to densities in two other regions of Kazakhstan: 'Betpak-Dala' of 0.11 birds km^{-2} (inter-period range 0.06–0.15) and 'Balkash', 0.10 (0.06–0.15) (Riou et al. 2011) and in China (average across five years 0.12 birds km^{-2}; [inter-annual range 0.05–0.20]) (Tourenq et al. 2005).

Analytical challenges

Inclusion of a random null variable following Boughey *et al.* (2011) clarified the interpretation of variable importance in cases when model selection ranked a variable high based on sum of AIC weights. We used GLMs to predict and map abundances—

an approach widely used and tested in ecological studies (Segurado and Araújo 2004; Elith and Graham 2009; Oppel et al. 2012). Predictors within the 'GLOBCOVER' model set failed to explain abundance of male houbara, probably owing to coarse resolution (approx. 700 m x 900 m) and potential lower ability of the GLC 2000 dataset to meaningfully classify subtle differences among desert vegetation and substrates. Thus freely available data could not substitute for detailed field measurements. A massive sampling effort was needed for the extrapolation of field measurements of shrub height and composition across the study area as well for the stratification by shrub assemblages of distance estimates. This gave a possibility to compare densities among plant assemblages, but did not substantially improve precision of the overall estimate, with 95% CIs only 1.5% narrower than those of the unstratified pooled estimate (Table 2), presumably due to proportionate sampling relative to assemblage extent. Maps of houbara male abundance based on the three remaining model sets showed different patterns, with 'Vegetation structure' giving the strongest agreement with the validation set.

Conclusion

This study is an initial step towards an understanding of the habitat requirements of and constraints on Asian Houbara populations on their breeding grounds, and is the first time that abundance of the species has been linked to particular plant assemblages. The more than two-fold difference in density between *Salsola*- and *Artemisia*-dominated habitats, and five-fold lower density in *Calligonum* habitats on unconsolidated sands, show the risks of extrapolating range-wide population estimates from local estimates of density, without accounting for desert-shrub/substrate composition. Habitats selected by males are likely to maximise the visibility and performance of their displays, as in male Great Bustards *Otis tarda* (Moreira et al. 2004) and male Bengal Floricans *Houbaropsis bengalensis* (Gray et al. 2009). However, the possibility remains that lower densities in some shrub assemblages reflects a lower suitability of these habitats for females, and thus a reduced attractiveness for males to congregate in such landscapes. Further work is required to determine what conditions the far more elusive females need for breeding, as their habitat and landscape preferences may differ somewhat from those of males (Hingrat et al. 2007), as in Bengal Florican (Gray et al. 2009). The southern Kyzylkum Desert is increasingly being targeted for energy (gas and oil) exploration (pers. obs.), and conservation biologists need a robust evidence base to ensure the best management for Uzbekistan's houbaras as their habitat experiences disruptions associated with economic development and infrastructural encroachment. As more information accumulates it will become possible to prioritise particular habitats for protection; evidence presented here suggests higher priority should be given to *Salsola*- and *Astragalus*-dominated areas than to *Calligonum* habitats on unconsolidated sands.

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References

Aghainajafizadeh, S., Hemami, M. R., Karami, M. and Dolman, P. M. 2010. Wintering habitat use by houbara bustard (*Chlamydotis macqueenii*) in steppes of Harat, central Iran. - Journal of Arid Environments 74: 912-917.

Aghanajafizadeh, S., Hemami, M. R., Naderi, G. and Heydari, F. 2012. Estimation of Houbara Bustard, *Chlamydotis macqueenii*, population density in the central Iranian steppes. - Zoology in the Middle East 56: 3-8.

Bartholomé, E. and Belward, A. S. 2005. GLC2000: a new approach to global land cover mapping from Earth observation data. - International Journal of Remote Sensing 26: 1959-1977.

Barton, K. 2013. MuMIn: multi-model inference. R package version 1.15.1, URL http://cran.r-project.org/web/packages/MuMIn/index.html.

Beehler, B. M. and Foster, M. S. 1988. Hotshots, hotspots, and female preference in the organization of lek mating systems. - The American Naturalist 131: 203-219.

Birdlife International. 2015. Species factsheet: *Chlamydotis macqueenii*. Downloaded from http://www.birdlife.org on 20/10/2015.

Boughey, K. L., Lake, I. R., Haysom, K. A. and Dolman, P. M. 2011. Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. - Biological Conservation 144: 2300-2310.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. and Thomas, L. 2001. Introduction to distance sampling: estimating abundance of biological populations*,* Oxford, Oxford University Press.

Burnham, K. P. and Anderson, D. R. (eds.). 2002. Model selection and multi-model inference. A practical information-theoretic approach.*,* Springer, New York.

Carrascal, L. M., Palomino, D., Seoane, J. and Alonso, C. L. 2008. Habitat use and population density of the houbara bustard *Chlamydotis undulata* in Fuerteventura (Canary Islands). - African Journal of Ecology 46: 291-302.

Chammem, M., Selmi, S., Khorchani, T. and Nouira, S. 2012. Using a capture-recapture approach for modelling the detectability and distribution of Houbara Bustard in southern Tunisia. - Bird Conservation International 22: 288-298.

Chargé, R., Sorci, G., Saint Jalme, M., Lesobre, L., Hingrat, Y., Lacroix, F. and Teplitsky, C. 2014. Does recognized genetic management in supportive breeding prevent genetic changes in life-history traits? - Evolutionary Applications 7: 521-532.

Combreau, O. and Launay, F. 1996. Activity rhythms of houbara bustards (*Chlamydotis undulata macqueenii*) in relation to some abiotic factors. - Journal of Arid Environments 33: 463-472.

Combreau, O., Launay, F. and Lawrence, M. 2001. An assessment of annual mortality rates in adult-sized migrant houbara bustards (*Chlamydotis undulata macqueenii*). - Animal Conservation 4: 133-141.

Combreau, O., Qiao, J., Lawrence, M., Gao, X., Yao, J., Yang, W. and Launay, F. 2002. Breeding success in a Houbara Bustard *Chlamydotis* [*undulata*] *macqueenii* population on the eastern fringe of the Jungar Basin, People's Republic of China. - Ibis 144: E45-E56.

Combreau, O. and Smith, T. R. 1997. Summer habitat selection by houbara bustards introduced in central Saudi Arabia. - Journal of Arid Environments 36: 149-160.

Combreau, O. and Smith, T. R. 1998. Release techniques and predation in the introduction of houbara bustards in Saudi Arabia. - Biological Conservation 84: 147-155.

Elith, J. and Graham, C. H. 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. - Ecography 32: 66-77.

Freckleton, R. P. 2002. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. - Journal of Animal Ecology 71: 542-545.

Gamoun, M. 2014. Grazing intensity effects on the vegetation in desert rangelands of Southern Tunisia. - Journal of Arid Land 6: 324-333.

Gaucher, P., Paillat, P., Chappuis, C., Saintjalme, M., Lotfikhah, F. and Wink, M. 1996. Taxonomy of the Houbara bustard *Chlamydotis undulata* subspecies considered on the basis of sexual display and genetic divergence. - Ibis 138: 273-282.

Gintzburger, G., Toderich, K. N., Mardonov, B. K. and Mahmudov, M. M. 2003. Rangelands of the arid and semi-arid zones in Uzbekistan*,* Paris, CIRAD, ICARDA.

Goriup, P. D. 1997. The world status of the houbara bustard *Chlamydotis undulata*. - Bird Conservation International 7: 373-397.

Graf, R. F., Bollmann, K., Suter, W. and Bugmann, H. 2005. The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. - Landscape Ecology 20: 703-717.

Gray, T. N. E., Chamnan, H., Collar, N. J. and Dolman, P. M. 2009. Sex-specific habitat use by a lekking bustard: conservation implications for the critically endangered Bengal Florican (*Houbaropsis bengalensis*) in an intensifying agroecosystem. - Auk 126: 112-122.

Gubin, B. 1992. Numbers,distribution and state of protection of the houbara bustard in the south of Kazakhstan. - Bustard Studies 5: 98-103.

Gubin, B. 2008. Numbers and seasonal distribution of Asian houbara (*Chlamydotis undulata macqueenii*) in Mangystau district (Kazakhstan) (in Russian). In: Spitsina, V. V. (ed.) Bustards of the Palearctic: breeding and conservation, Moscow, pp. 108-129.

Gubin, B. M. 2004. Drofa-krasotka (Houbara Bustard) (in Russian)*,* Almaty Kolor.

Hingrat, Y., Jalme, M. S., Chalah, T., Orhant, N. and Lacroix, F. 2008. Environmental and social constraints on breeding site selection. Does the exploded-lek and hotspot model apply to the Houbara bustard *Chlamydotis undulata undulata*? - Journal of Avian Biology 39: 393-404.

Hingrat, Y., Saint Jalme, M., Ysnel, F., Le Nuz, E. and Lacroix, F. 2007. Habitat use and mating system of the houbara bustard (*Chlamydotis undulata undulata*) in a semi-deserticarea of North Africa: implications for conservation. - Journal of Ornithology 148: 39-52.

Hirzel, A. H. and Lay, G. L. 2008. Habitat suitability modelling and niche theory. - Journal of Applied Ecology 45: 1372-1381.

Johnston, A., Thaxter, C. B., Austin, G. E., Cook, A. S. C. P., Humphreys, E. M., Still, D. A., Mackay, A., Irvine, R., Webb, A. and Burton, N. H. K. 2015. Modelling the abundance and distribution of marine birds accounting for uncertain species identification. - Journal of Applied Ecology 52: 150-160.

Koshkin, M. A., Collar, N. J. and Dolman, P. M. 2014. Do sheep affect distribution and habitat of Asian Houbara *Chlamydotis macqueenii*? - Journal of Arid Environments 103: 53-62.

Launay, F., Loughland, R. and Mukhina, E. A. 1997a. Preliminary observations of the incubation and covey behaviour of Houbara Bustard *Chlamydotis undulata macqueeni*. - Sandgrouse 19: 51-55.

Launay, F., Roshier, D., Loughland, R. and Aspinall, S. J. 1997b. Habitat use by houbara bustard (*Chlamydotis undulata macqueenii*) in arid shrubland in the United Arab Emirates. - Journal of Arid Environments 35: 111-121.

Le Cuziat, J., Lacroix, F., Roche, P., Vidal, E., Medail, F., Orhant, N. and Beranger, P. M. 2005a. Landscape and human influences on the distribution of the endangered North African houbara bustard (*Chlamydotis undulata undulata*) in Eastern Morocco. - Animal Conservation 8: 143-152.

Le Cuziat, J., Vidal, E., Roche, P. and Lacroix, F. 2005b. Human activities affect the potential distribution of the Houbara Bustard *Chlamydotis undulata undulata*. - Ardeola 52: 21-30.

Mitropolsky, O. V., Mukhina, E. A. and Nazarov, O. P. 1996. Houbara Bustard *Chlamydotis undulata\macqueenii* in Uzbekistan. First Meeting of the IUCN SSC Houbara Bustard Working Group, Muscat, Oman.

Moreira, F., Morgado, R. and Arthur, S. 2004. Great bustard *Otis tarda* habitat selection in relation to agricultural use in southern Portugal. - Wildlife Biology 10: 251-260.

NASA. 2011. ASTER Global Digital Elevation Model V2. - The Ministry of Economy, Trade and Industry (METI) of Japan and the United States National Aeronautics and Space Administration (NASA).

Oppel, S., Meirinho, A., Ramírez, I., Gardner, B., O'connell, A. F., Miller, P. I. and Louzao, M. 2012. Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. - Biological Conservation 156: 94-104.

Peterson, A. T. 2006. Uses and requirements of ecological niche models and related distributional models. - Biodiversity Informatics 3: 59-77.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, URL http://www.R-project.org/. Vienna, Austria.

Rachkovskaya, E. I. 1995. Vegetation map of Kazakhstan and Middle Asia (Desert region). Russian Academy of Sciences, Saint Petersburg.

Renwick, A. R., Massimino, D., Newson, S. E., Chamberlain, D. E., Pearce-Higgins, J. W. and Johnston, A. 2012. Modelling changes in species' abundance in response to projected climate change. - Diversity and Distributions 18: 121-132.

Riou, S., Judas, J., Lawrence, M., Pole, S. and Combreau, O. 2011. A 10-year assessment of Asian Houbara Bustard populations: trends in Kazakhstan reveal important regional differences. - Bird Conservation International 21: 134-141.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. - Biometrics 60: 108-115.

Seddon, P. J., Saint Jalme, M., Van Heezik, Y., Paillat, P., Gaucher, P. and Combreau, O. 1995. Restoration of houbara bustard populations in Saudi Arabia: developments and future directions. - Oryx 29: 136-142.

Segurado, P. and Araújo, M. B. 2004. An evaluation of methods for modelling species distributions. - Journal of Biogeography 31: 1555-1568.

Simpson, E. H. 1949. Measurement of diversity. - Nature 163: 688.

Tourenq, C., Combreau, O., Lawrence, M., Pole, S. B., Spalton, A., Gao, X. J., Al Baidani, M. and Launay, F. 2005. Alarming houbara bustard population trends in Asia. - Biological Conservation 121: 1-8.

Tourenq, C., Combreau, O., Pole, S. B., Lawrence, M., Ageyev, V. S., Karpov, A. A. and Launay, F. 2004. Monitoring of Asian houbara bustard *Chlamydotis macqueenii* populations in Kazakhstan reveals dramatic decline. - Oryx 38: 62-67.

van Heezik, Y. and Seddon, P. J. 1999. Seasonal changes in habitat use by Houbara Bustards *Chlamydotis undulata macqueenii* in northern Saudi Arabia. - Ibis 141: 208-215.

Waber, K., Spencer, J. and Dolman, P. M. 2013. Achieving landscape-scale deer management for biodiversity conservation: The need to consider sources and sinks. - Journal of Wildlife Management 77: 726-736.

Yang, W. K., Qiao, J. F., Combreau, O., Gao, X. Y. and Zhong, W. Q. 2002a. Display-sites selection by houbara bustard (*Chlamydotis undulata macqueenii*) in Mori, Xinjiang, People's Republic of China. - Journal of Arid Environments 51: 625-631.

Yang, W. K., Qiao, J. F., Combreau, O., Yao, J., Gao, X. Y. and Zhong, W. Q. 2002b. Breeding habitat selection by houbara bustard (*Chlamydotis undulata macqueenii*) in Mori, Xinjiang, China. - Science in China Series D-Earth Sciences 45: 1-10.

Chapter 3 – Supplementary online materials (SOM)

1. Vegetation classification

At each point count location, on each of the four vegetation line-intercepts the species and height of each shrub touching the line was recorded to 1 cm accuracy, following Koshkin et al. (2014). *Shrub height* (a measure of houbara concealment) was calculated as the mean height across 28 shrub species, excluding the dwarf *Salsola gemmascens* and *Nanophiton erinaceum* (mean height <12 cm), pooling line intercepts for each point count (n = 231).

Additional vegetation data collected under the same protocols were used in reclassification and spatial interpolation of shrub assemblages. These comprised samples collected (1) during May–June 2012 at 167 random points (each comprising three parallel 50m line-intercepts, with 25 m spacing) (Forsstrom 2012); (2) in May–June 2013–14 at 323 houbara nests or randomly selected control locations (each comprising four 50 m line intercepts, radiating from nest cup location) (2013: n = 128; 2014: n = 195); and (3) in June 2012 along 96 10 km transects (each sample comprising four 50m line-intercepts, with 2 km spacing), with pooled values attributed to the midpoint of each transect (Koshkin et al. 2014).

Composite samples (of shrub frequency per 200 m) were classified by hierarchical cluster analysis considering the eight most abundant shrub species (41,674 shrubs, 63.2% of all shrubs measured) across the composite dataset of 817 sampling locations. Cluster analysis was performed on the Bray Curtis similarity matrix of shrub abundances (frequency per 200 m, square-rooted), using average-linkage clustering and a 50% similarity level to select the four most common assemblages (87% of all samples), in PRIMER v. 6.1.10 (Clarke 1993; Peet and Roberts 2013).

The following five shrub assemblages were identified from the cluster analysis: (a) '*Artemisia*' located on gypseous clay soils in areas at higher elevation (mean = 266.8 ± 2.7 m a.s.l.), often intersected by wadis and valleys and largely comprising *Artemisia diffusa* (93.3% of all shrubs recorded in this assemblage) forming a homogenous shrub vegetation of relatively low height; (b) '*Salsola arbuscula*', on gypseous and halophytic soils, again comprising a relatively high abundance of *A. diffusa* (58.8%) but characterised by taller *S. arbuscula* (14.9%) and shorter *S. rigida* (14.8%); (c) '*Salsola rigida*', on halophytic soils with shrub communities dominated by *S. rigida* (39.1%) and the dwarf *S. gemmascens* (21.8%); (d) '*Astragalus*' on semi-consolidated sands, again with high density of *Salsola* spp. (46.4%) but characterised by co-dominant *A. villosissimus* (18.3%) and *Convolvulus hamadae* (23.1%); and (e) '*Calligonum*' on weakly consolidated and drifting sands, supporting a diverse shrub assemblage, again with high frequency of *A. villosissimus* (18.1%) and *C. hamadae* (51.1%), but characterised by *Calligonum* spp. (10.1%). Nonmetric multidimensional scaling analysis supports the distinctive composition of each of these assemblages (SOM Fig.S1).

Assemblage identity was then assigned to each location (n = 765, excluding locations assigned to smaller classes, totalling <1% samples) and a polygon shapefile created using the 'Thiessen polygons' tool (Arc Map 10.1). This tool was used to divide the area covered by the point features into 'Thiessen' polygons or proximal zones. Each of these polygons defines an area of influence around its sample point, so that any location inside the polygon is closer to that point than any of the other sample points. To smooth fine-detail Thiessen polygons (n = 748 polygons; mean area = 44.5 km^2, *SD* = 134.5) and to create a simplified map of the distribution of shrub assemblages (n = 31 polygons; mean area = 507.4 km^2, *SD* = 667.6; SOM Fig.S2 c), suitable for stratification of houbara density in distance analysis we used 'Polygons to raster', 'Region group', 'Extract' and 'Nibble' tools in Arc Map 10.1.

2. Testing detectability covariates in distance analysis of houbara density

Date was expected to affect detectability, as houbara were assumed to be more difficult to see later in the season owing to decrease in display intensity (pers. obs.). We therefore explored the effects of including *date* as a continuous and *visit* (first or second visit to a point count) as a categorical covariate in separate models. Activity and therefore detectability were observed to be greater soon after sunrise, to decline by mid-morning and then to increase again towards sunset. Time was therefore included as a quadratic term (*time* + *time*^{2}) to account for non-linear change in birds' activity during the day, as a categorical variable (*time cat.*; 1 = morning, 2 = afternoon) and as a continuous variable relative to sunrise/sunset (*time continuous*; minutes after sunrise/before sunset). In conditions of strong wind males reduce display activity (pers. obs.), so strength of wind was also considered (*wind*). Finally, we considered *shrub height* when exploring detectability, as houbaras may be less visible with taller or denser vegetation. All covariates were checked for collinearity and only uncorrelated pairs were included into the same Distance models, with the sampling fraction specified as 1.0. Half-normal and hazard-rate detection functions were fitted examining both cosine and polynomial adjustments (simple or hermite) and that with the lowest Akaike Information Criterion (AIC) was selected, following Buckland et al. (2001). Separate sets of models were examined after truncation of either 5% or 10% of the most distant observations, and that providing the greater precision to the density estimate was selected.

3. Sheep density analysis

Sheep density was estimated by distance analysis, fitting uniform, half-normal and hazard-rate detection functions which examine both cosine and polynomial adjustments (simple or hermite), following Buckland et al. (2001). The detection model with the lowest Akaike Information Criterion (AIC) was selected; when there were two or more best competing models (with ΔAIC <2), model-averaging was undertaken. Separate sets of models were examined after truncation of either 5% or 10% of the most distant observations, following Buckland et al. (2001) and the truncation that provided the greater precision (i.e. CI) to the density estimate was selected. A total of 331 sheep groups were observed, with mean group size of 181.1 (*SD* = 135.9, range 2–750). Whether or not a sheep flock is observed at a particularly location on a visit is affected by chance sampling error and daily movements of flocks within their home range (with movements of $\approx$ 5 km day^{-1}). As we were interested in the seasonal mean density of sheep around point count locations, an interpolated density surface was created by Inverse Distance Weighting (with 500 m raster resolution) from transect-specific density values assigned to transect centroids. This captured the larger scale gradients of sheep density across the desert as determined by access to water, and density of pastoralists' camps (see Fig S2 a). Mean sheep density around each point (*sheep density*) was then extracted from the interpolated surface across a 2 km radius buffers using 'Zonal statistics as a table' tool in Arc Map 10.1.

4. Floaters

Binomial mixture models (BMM) were not used to control for imperfect detection of houbara on visits, as the assumption of population closure was considered likely to be violated due to the relatively long re-sampling interval between repeat visits to the same point (mean = 27.2 days, SD = 8.3) and likelihood of individual movement due to the presence of a number of groups that may not hold a fixed territory throughout the breeding season. These included:

a) Floaters (defined as individual males that are members of the study population, but that are not holding a static territory and are mobile during the breeding season (Brown 1969)).

Satellite telemetry data show that subadult males utilised a much larger area throughout the breeding season in Bukhara (n = 4 males, mean = 233 km^2, range = 100–400 km^2) than adult males (n = 8 male/seasons, mean = 12 km^2, range = 4–25) (MK, unpublished data). With each point count covering just over 6 km^2 and with minimum distances between point count location of 4 km these birds have higher chances of being recorded on more than one point count within a season, than older males faithful to their leks.

b) Passage birds (defined as individuals on passage to other breeding populations, stopping over in Bukhara).

Extensive satellite tagging by Combreau et al. (2011) demonstrated that most houbara tagged in central and eastern Kazakhstan and in eastern China are crossing Bukhara district during autumn migration to their wintering grounds in Pakistan. Data from the same study also show that six males ringed as adults in Kazakhstan or China crossed Uzbekistan between 1 March and 3 June during their spring migration, which overlaps with the breeding period in our study area (O. Combreau unpublished data, pers. comm.). These data (Combreau unpublished) also suggest two peaks of houbara migration through Uzbekistan, one in mid-March (thus largely before sampling in our point count data) and another at the end of April during sampling of this study.

c) Subadults with arrested migration (defined as subadults from more northern populations, with arrested migration in Bukhara district)

A juvenile fitted with a satellite transmitter in the pre-migratory autumn period (October) in 2011 in Bukhara district spent the first few months of the 2012 breeding season slowly migrating north from its wintering grounds in south-eastern Iran and spent the rest of the breeding season (June–October) in Turkmenistan, 400 km south of its first-autumn capture location. However during the two subsequent years (2012–2013) this individual used an area of 25 km² in Bukhara (most likely displaying at the same lek) (MK unpublished). Similarly, we expect that some subadults from breeding grounds further north in Kazakhstan and China may move slowly through (thus acting as floaters during our sampling period) and potentially oversummer in Uzbekistan, as shown for one subadult houbara from China (Combreau et al. 2011).

Supplementary tables

Table S1: Results of conventional distance sampling (CDS) and multiple-covariates distance sampling (MCDS) models testing for the effect of time and date (A) and other factors (B) on detectability of houbara (males and unsexed birds only) on point counts (n=231). Change in Akaike Information Criterion (corrected for small sample size, ΔAIC) was used to compare each candidate model with the best model. Distances were truncated at 1,400 m to consider only distances measured by rangefinder. In (B), models of other factors (shrub height, wind, topographic rugosity) include the best supported effects of time and date from models considered in (A). Abbreviations: gr.si. = group size; Enc. Rate = encounter rate; EDR = effective detection radius

Covariate	**Density (inds/km^2) (95% CI)**	**AICc**	**ΔAICc**	**EDR (metres) (95% CI)**	**Mean gr. si.**	**Enc. rate**
CDS analysis (no covariates)	0.135 (0.111-0.164)	3109.3	5.6	1057 (959-1164)	1.01	0.46
MDCS analysis (covariates)					1.01	0.46
A						
Time +Time^2	0.137 (0.125-0.151)	3109.6	5.9	1052 (1004-1104)		
Time cat	0.137 (0.125-0.151)	3107.4	3.7	1052 (1004-1102)		
Time +Time^2+Time^3	0.137 (0.125-0.151)	3111.6	7.9	1051 (1002-1102)		
Time_min	0.135 (0.123-0.148)	3111.3	7.6	1059 (1013-1108)		
Time_min+Time_cat	0.137 (0.124-0.151)	3109.5	5.8	1052 (1003-1102)		
Date	0.138 (0.125-0.152)	3105.9	2.2	1050 (1001-1102)		
Date + Time + Time^2	0.142 (0.127-0.158)	**3105.1**	**1.4**	1034 (982-1090)		
Date + Time cat	0.140 (0.127-0.156)	**3104.7**	**1**	1039 (988-1092)		
Visit	0.137 (0.124-0.151)	3106.4	2.7	1049 (1001-1100)		
Visit +Time cat	0.140 (0.126-0.154)	**3103.7**	**0**	1036 (985-1091)		
Visit +Time + Time^2	0.140 (0.126-0.156)	**3105.0**	**1.3**	1033 (980-1088)		
B						
Visit +Time cat + Shrub height	0.139 (0.126-0.155)	**3105.4**	**1.7**	1036 (983-1091)		
Visit +Time cat + SD DEM	0.140 (0.126-0.155)	**3105.5**	**1.8**	1035 (983-1090)		
Visit +Time cat + Wind	0.140 (0.124-0.155)	**3105.4**	**1.7**	1036 (984-1091)		
Visit +Time cat + Wind + DEM	0.142 (0.127-0.158)	3107.3	3.6	1035 (982-1091)		
Visit +Time cat + Wind + ShrubH	0.139 (0.125-0.155)	3107.4	3.7	1037 (983-1099)		
Visit +Time cat + SD DEM + ShrubH	0.141 (0.126-0.156)	3107.4	3.7	1035 (982-1091)		
Visit +Time cat + Wind + SD DEM + ShrubH	0.149 (0.126-0.156)	3109.2	5.5	1035 (981-1092)		

Supplementary figures

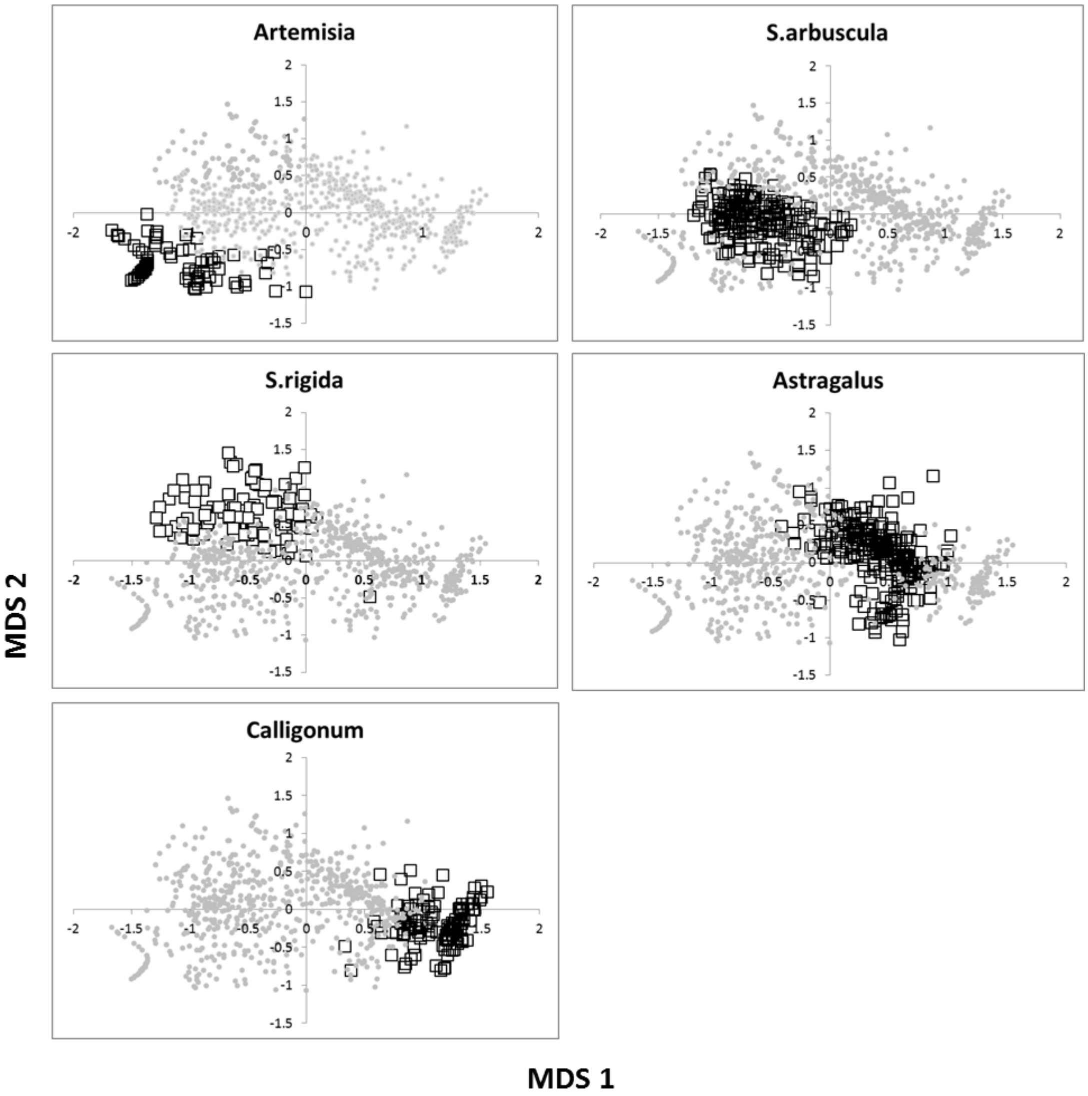

Fig. S1 Nonmetric Multidimensional Scaling (MDS) loadings for each sampling location (n = 817) for each shrub assemblage.

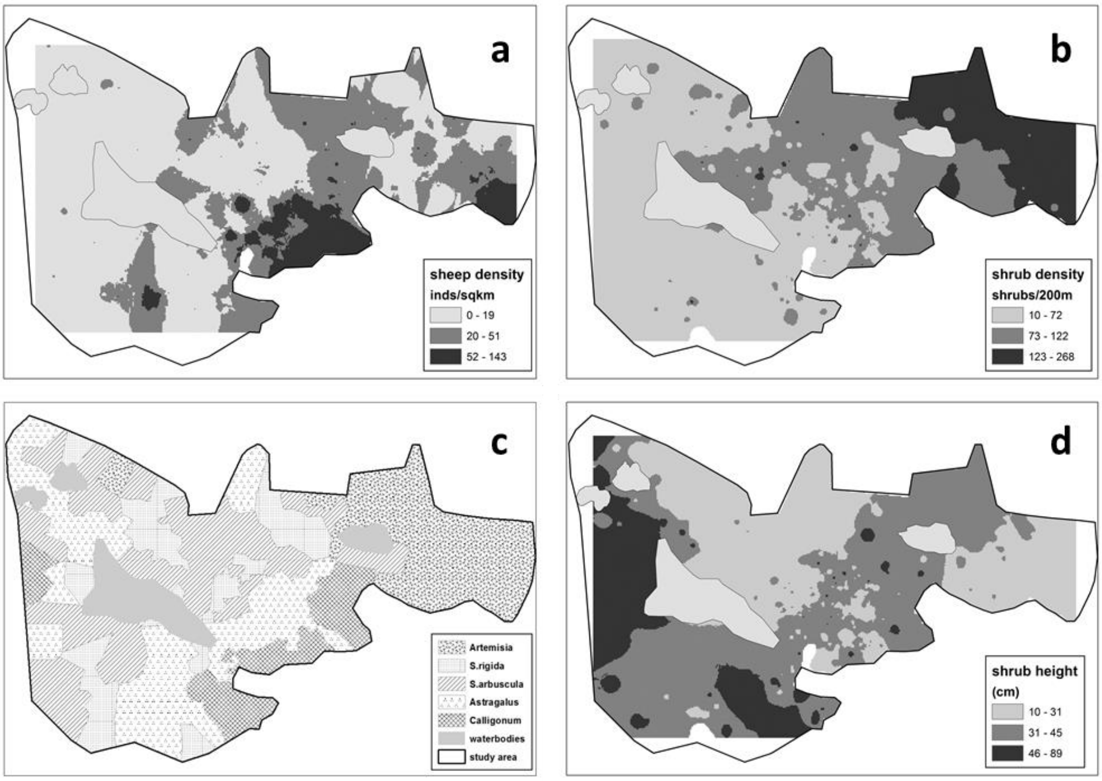

Fig. S2 Study area showing gradients of a) sheep density, b) shrub density, distribution of c) shrub assemblages, and gradients of d) shrub height.

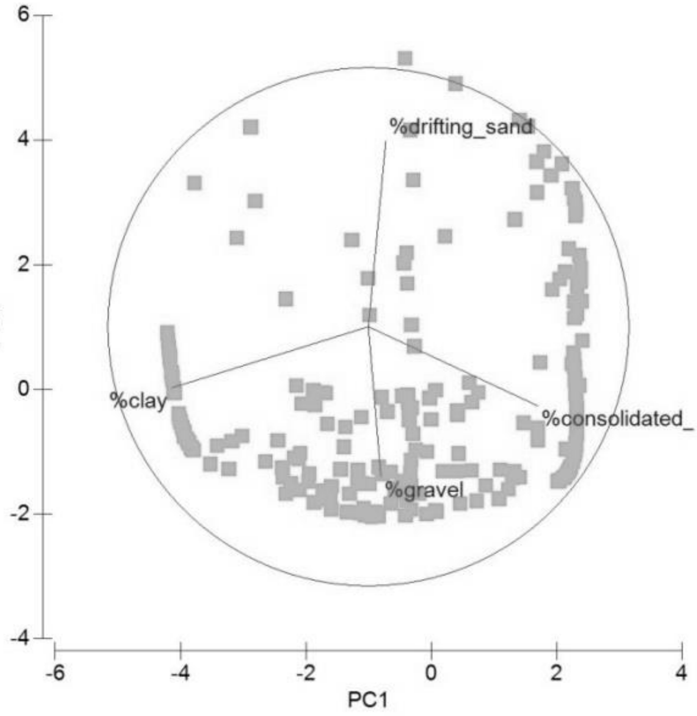

Fig. S3 Sample scores on the first two Principal Component Analyses (PCA) axes of substrate (data from two years – 2012–2013), showing change from clay cover (negative) to consolidated sand (positive) along PC1 and change from gravel (negative) to drifting sand (positive) along PC2.

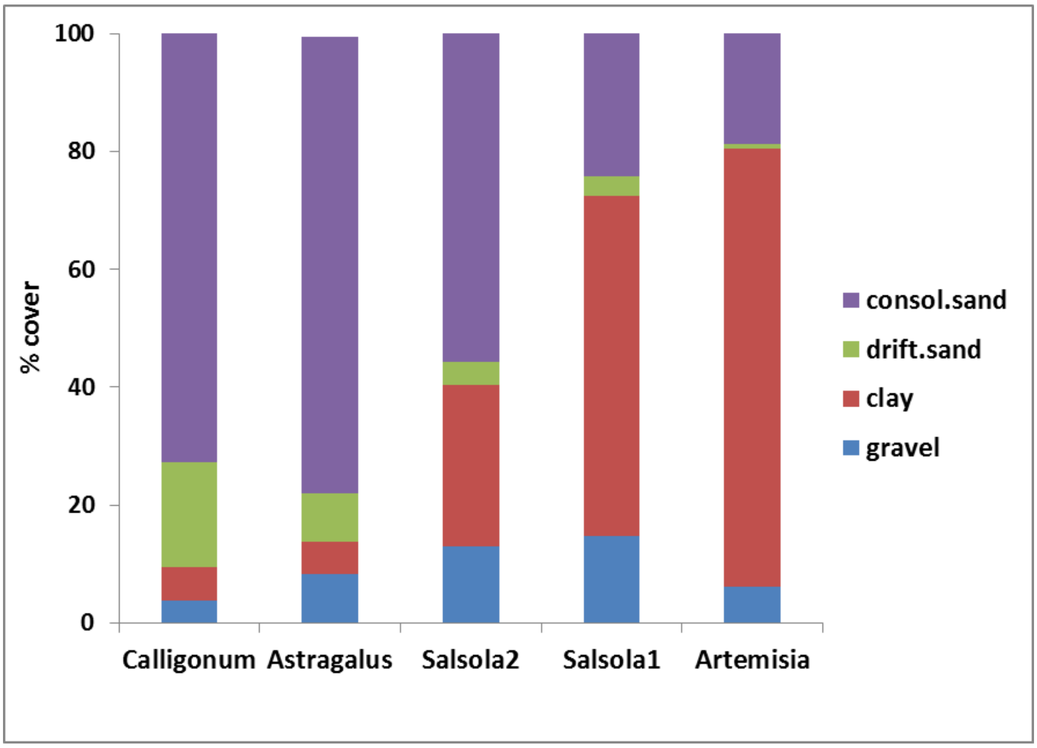

Fig. S4 Mean % cover of each of four substrate classes for each shrub assemblage, for 364 sampling locations.

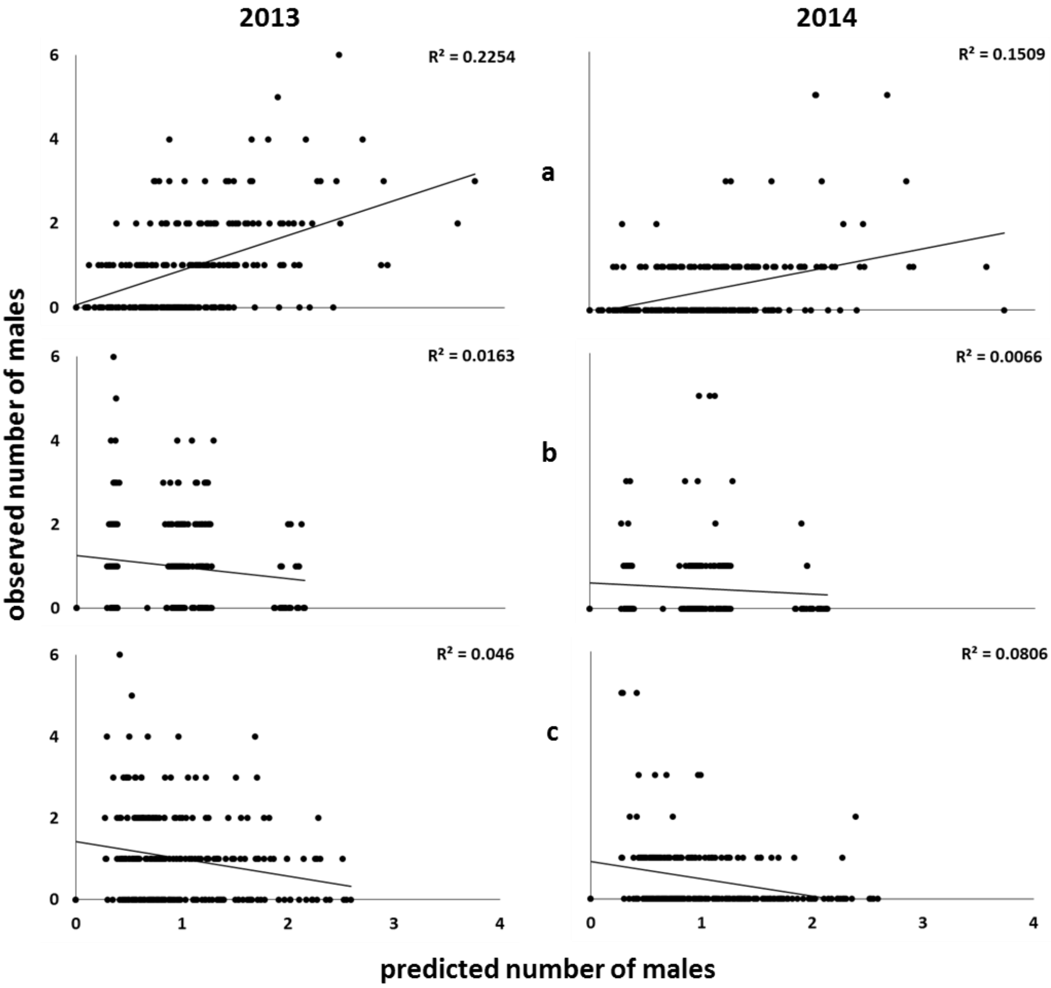

Fig. S5 Number of males observed at point counts in 2014 (maximum count per point across two visits), shown in relation to numbers predicted from GLMs of shrub height (a), shrub assemblage (b) and shrub MDS (c) (value extracted per point from maps of predicted abundance (grid resolution 1,836 m x 1,836 m), from models calibrated with data from point counts conducted in 2013.

Supplementary references

Brown, J. L. 1969. The buffer effect and productivity in tit populations. - Am.Nat. 103: 347-354.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. and Thomas, L. 2001. Introduction to distance sampling: estimating abundance of biological populations, Oxford, Oxford University Press.

Clarke, K. R. 1993. Nonparametric multivariate analyses of change in community structure. - Australian Journal of Ecology 18: 117-143.

Combreau, O., Riou, S., Judas, J., Lawrence, M. and Launay, F. 2011. Migratory pathways and connectivity in Asian Houbara Bustards: evidence from 15 years of satellite tracking. - PlosOne 6.

Forsstrom, S. 2012. Response of the long-clawed ground squirrel (*Spermophilopsis leptodactylus*) to sheep grazing on a semi-arid rangeland in southern Uzbekistan. School of Biological Sciences. University of East Anglia, Norwich, pp. 48.

Koshkin, M. A., Collar, N. J. and Dolman, P. M. 2014. Do sheep affect distribution and habitat of Asian Houbara *Chlamydotis macqueenii*? - Journal of Arid Environments 103: 53-62.

Peet, R. K. and Roberts, D. W. 2013. Classification of natural and semi-natural vegetation. Vegetation Ecology. John Wiley & Sons, Ltd, pp. 28-70.

Chapter 4

Effects of habitat and livestock on nesting success of the declining Asian houbara *Chlamydotis macqueenii*

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Abstract

To inform population support measures for the over-exploited, declining Asian houbara *Chlamydotis macqueenii* (IUCN Vulnerable) we examined potential habitat and land-use effects on wild nest productivity in the Kyzylkum Desert, Uzbekistan. We monitored 177 nests across different semi-arid shrub assemblages (clay-sand and salinity gradients) and a range of livestock densities (0–80 km-2). Nest success (mean 51.4%, 95% CI 42.4–60.4%) was similar across four years; predation caused 85% of those failures for which the cause was known, and only three nests were trampled by livestock. Nesting begins within a few weeks of arrival when food appears scarce, but later nests were more likely to fail due to emergence of a key predator, suggesting foraging conditions on wintering and passage sites may be important for nesting productivity. Nest success was similar across three shrub assemblages and was unrelated to landscape rugosity, shrub frequency or livestock density, but was greater in areas with taller mean shrub height (range 13–67 cm) within 50 m. Clutch size (mean = 3.2 eggs) and per-egg hatchability in successful nests (87.5%) did not differ with laying date, shrub assemblage or livestock density. We therefore found no evidence that livestock density reduced nest productivity across the range examined, while differing shrub assemblages appeared to offer similar habitat quality. Asian houbara appear well-adapted to a range of semi-desert habitats and tolerate moderate disturbance by pastoralism. No obvious in situ mitigation measures arise from these findings, leaving regulation based on demographic analysis as the key requirement to render hunting sustainable.

Introduction

Interventions to conserve species are more effective when informed by demographic measures of relevant life-history, seasonal and, for migratory species, geographic stages (Robinson et al. 2004; Sutherland et al. 2004). Even when mitigating negative demographic impacts at one stage proves impracticable, such information may support compensatory measures (O'Brien et al. 2006; Perrins et al. 1993; Wright et al. 2009). For example, elevated anthropogenic mortality along a migration corridor is challenging to mitigate, but might be offset by enhancing breeding productivity. For species breeding across heterogeneous environments, prioritisation of such measures requires an understanding of the potential demographic effects of land-use and landscape composition to identify areas that determine regional-scale demography (Dolman 2012; Waber et al. 2013). Here we undertake such an evaluation, using as a model the Asian houbara *Chlamydotis macqueenii* (IUCN status Vulnerable: BirdLife International 2015), a bustard of desert and semi-arid landscapes and the chief quarry of Arab falconers. Asian houbara have suffered near-extirpation of resident populations in the Arabian Peninsula and major declines across Central Asia, primarily as a consequence of unregulated hunting and trapping during migration and winter (Riou et al. 2011; Tourenq et al. 2005), with degradation of breeding habitat considered a further factor (Lavee 1988).

Captive breeding is used in parts of the range of both Asian and African houbara *C. undulata* to re-establish or reinforce exploited wild populations, increasingly through large-scale releases (Chargé et al. 2014; Hardouin et al. 2015; Islam et al. 2012). However, the demographic consequences of such releases for reinforced houbara populations are unreported. Selection in captivity on a range of physiological, reproductive and behavioural traits has been reported (Chargé et al. 2014), but the resulting genetic, disease and domestication risks to wild populations (Dolman et al. 2015; Frankham 2008; Snyder et al. 1996; Williams and Hoffman 2009) are unknown. Given such risks, opportunities for *in situ* conservation measures should be evaluated, particularly as the value of captive breeding and release may diminish without simultaneous, effective *in situ* measures (Dolman et al. 2015). However, the evidence base for selecting management interventions to support or enhance productivity of wild populations is currently weak.

Asian houbara (hereafter 'houbara') breed across a wide range of vegetation types and landscapes, varying with drainage, landform and substrate, from consolidated sands to clay saltpans (Gubin 2004), which differ in shrub height and composition (Koshkin et al. 2014; Koshkin et al. in press). Nest success of wild houbara has been quantified (Combreau and Launay 1999; Combreau et al. 2002; Lavee 1988) and nest micro-site selection investigated (Aghanajafizadeh et al. 2012; Yang et al. 2003), but whether productivity varies with habitat differences or livestock levels remains unknown. Rangelands occupy most houbara breeding habitat in Central Asia (Robinson et al. 2007), with obvious potential to impact populations through habitat modification, livestock trampling and disturbance of nests. However, as livestock are vital to local livelihoods and regional economies (Gintzburger et al. 2003; Kerven et al. 2006), robust evidence of their demographic effects on houbara needs to inform any management intervention. In Israel, expert opinion suggested that livestock grazing negatively impacts nest success through disturbance (Lavee 1988) and, in Morocco, livestock concentrations may restrict African houbara access to suitable areas (Le Cuziat et al. 2005b). In Morocco and Fuerteventura, breeding African houbara avoid major roads, human settlements and sheep camps (Carrascal et al. 2008; Hingrat et al. 2008; Le Cuziat et al. 2005a), but whether these anthropogenic factors influence productivity has not been examined. Although numbers and distribution of male houbara showed no response to low and moderate sheep densities in the southern Kyzylkum, Uzbekistan (Koshkin et al. 2014; Koshkin et al. in press), livestock impacts on nesting are unknown.

Using data from 177 Asian houbara nests monitored in the Kyzylkum over four years (2012–2015), we: (i) quantify clutch size, nest success and hatchability (which together determine nest productivity), and their variation within the breeding season and across years; (ii) test for the effects of land-use and habitat on these components of nest productivity, particularly the influences of shrub species composition and of sheep density, and (iii) assess the causes of nest failure. We expected that the findings of this analysis would have significant implications for appropriate long-term houbara conservation and management, as well as for priorities for further research.

Methods

Study area

The study area (39.34–40.56°N 62.21–65.20°E) covers 14,300 km^2 of predominantly flat houbara habitat, comprising drought-resistant and halophytic shrub vegetation, in the southern Kyzylkum Desert, Bukhara District, Uzbekistan. Grazing by mixed flocks of sheep and goats (hereafter 'sheep', as these dominate) is limited by the distribution of functioning wells, major roads and trackways used for water transportation (Koshkin et al. 2014). Large areas of desert, particularly with limited accessibility to water, are grazed only in spring during lambing, when sheep exploit ephemeral graminoids (*Carex physodes* and *Bromus* spp.). From mid-May, after the main houbara nesting period is complete, sheep are withdrawn to villages, agricultural areas or permanent water sources. Owing to the short duration of pastoralism and absence of winter browsing, sheep have a limited impact on shrub vegetation (Koshkin et al. 2014), but extensive grazing of mobile flocks may potentially disrupt nesting houbara. Although areas closer to settlements and permanent water sources, with higher densities of wells and camps, support larger numbers of sheep, much of the surrounding desert is under-utilised (Koshkin et al. 2014). This spatial variation in sheep density allowed livestock effects to be examined.

Nest searching and monitoring

Houbara nests were located between 20 March (all years) and 30 April (2012) or 10 May (2013, 2014 and 2015) by searching for female tracks; searches between 11:00 and 15:00 were excluded to avoid risk to eggs through exposure to high temperatures. Modest numbers of captive-bred houbara have been released in Bukhara in recent years, so it is possible that some nesting birds are of captive origin. Not all incubating females were checked for metal rings, but evidence from catching and nest-cameras suggests that the proportion of released captive-bred birds among females breeding in Bukhara is currently low (e.g. 1 in a sample of 50, 2.0 %, 95% CI: 3.7%), consistent with low numbers released relative to the large extant population (Koshkin et al. in press) and low subsequent over-winter survival of released birds (Burnside et al. in press). Searches traversed a variety of substrates (consolidated and weakly consolidated sand, clay) across five shrub assemblages (see below); cultivated areas and drifting dunes were excluded, as they hold very low densities of houbara during the breeding season (Koshkin et al. 2014). Although search effort was widely distributed, the probability of finding nests through tracking was greater in sandy areas; searches on clay were possible only when they held scattered drifts of sand. Thus the distribution of nests monitored did not represent relative nesting density across habitats and therefore we do not infer habitat preferences. Nevertheless, environmental determinants of productivity per nesting attempt could be examined, as sufficient nests were located in each habitat. Nests were also located by tracking of 25 wild females carrying satellite transmitters (30 g PTT-100

Argos/GPS solar-powered; Microwave Telemetry Inc.) caught using lines of leg snares, set around an initial nest found during standard fieldwork. As catching of females was considered likely to cause nest desertion, or at least prolonged exposure of the eggs, these females were caught early in the season to maximise their chances of re-nesting, with clutches removed for artificial incubation at a specialist houbara breeding centre; this terminated monitoring of the initial nesting attempt. Subsequent nests of these females (in the same and successive years) were visited under standard protocols.

We found 177 nests, of which 20, 44, 52 and 61 were found in 2012, 2013, 2014 and 2015 respectively (Fig.1). Of these, 46 were found using GPS locations from 25 females tracked by satellite telemetry, but only 10 of these females contributed more than one nest to the data. Ten nests were found outside the area sampled for vegetation and sheep density (with outcome and/or clutch size unknown for six of these) and were therefore excluded from analyses of environmental effects. Three nests where females were flushed by car were also excluded from analyses of nest success, as these were considered to have been compromised (all were predated within one day). Of the remaining sample of 164, 64 were found in *Astragalus*, 19 in *Salsola rigida,* 78 in *Salsola arbuscula* and only three in *Artemisia* shrub vegetation. Nests found in *Artemisia* were excluded from models that included '*shrub assemblage*' owing to low sample size. This provided 161 nests for modelling of environmental effects, or 164 where analyses included MDS2 instead of '*shrub assemblage*', with sample sizes for differing life history stages of: clutch size (n = 159 or 162 respectively), nest success (n = 151 or 154) and hatchability (n = 68 or 71).

In 2012, eggs were not measured, and laying date was estimated from hatching date and duration of incubation (23 days: Combreau et al. 2002) with a range of uncertainty for nests that failed, following Mallord et al. (2007). In 2013–2015, hatching and thus laying dates were predicted from egg dimensions and weight (measured at the time the nest was found) following the weight-loss equation from Hoyt (1979), using species-specific weight coefficient K_w = 0.00055 and assuming linear weight-loss of 17.4 % across incubation, following Combreau et al. (2002). After finding, subsequent monitoring visits were made at intervals of five or six days, and then two days before and one day after the predicted hatching date. As it is important to minimise cues that may influence the ability of predators to detect nests, at the first visit (when eggs were measured and weighed) fieldworkers did not kneel at the nest and left using the same route which was swept (using local vegetation) to remove all footprints. On all subsequent visits prior to completion or failure, observations were made remotely through binoculars and at no time did fieldworkers approach closer than 10 m. For further details of nest monitoring, see Online resources (section 2).

Nest outcome was inferred through signs within and around the nest scrape. A nest was considered failed if it was found empty prior to the predicted hatching date or with signs of predation or trampling; and successful if at least one egg hatched, based on signs of a successful outcome (Online resources, section 3). In 2014 and 2015, nest-cameras and temperature loggers were used in a total of 36 nests to confirm outcomes inferred from field signs and to refine estimated completion date (Online resources, section 3). Nest-cameras, equipped with infra-red (940 nm) emitting diodes for night surveillance, were set to record video continuously; to reduce disturbance, cameras were deployed during the second visit to a nest at a distance of > 1 m from the scrape, with installation taking < 20 minutes. Battery units were buried approximately 10 m from the nest to reduce disturbance during maintenance visits (every five days). Temperature loggers (I-buttons, DS1921G-F5 thermochrons) capable of recording temperature every 15 seconds over the incubation period were placed in nests at first finding and left until after completion of the nesting attempt, with one in substrate 1 cm beneath the eggs and a second at the same depth some 30 cm from the scrape to record ambient temperature, so that times of incubation could be determined. When a nest had no logger or camera and exact day of finishing was unknown, the mid-point between the final and penultimate visit was taken as the end date (Mayfield 1975).

Habitat and land-use variables

Six candidate habitat and land-use variables were examined for their potential influence on clutch size, hatchability and nest success (Table 1). Structure and composition of shrub vegetation in the vicinity of the nest were recorded along four 50 m cardinally directed line intercepts radiating from the scrape, to represent habitat at the scale of nest-site placement within the home range. Along each line intercept, the species and height (to 1 cm) of each shrub touching the line was recorded following Koshkin et al. (2014), pooling data for each nest (hereafter 'composite samples'). Mean *shrub height* (measure of vegetation structure) and square-root transformed *shrub frequency* (an index of vegetation cover per composite 200 m sample) were calculated across 19 shrub species (excluding the dwarf species *Salsola gemascens* and *Nanophyton erinaceum* with mean height <12 cm). To avoid disturbance, vegetation measurements were taken after nest outcomes were known.

Table 1. Candidate habitat and land-use variables for models of nest success, clutch size and hatchability.

Variable name	**Description**	**Type of data**
***a priori* covariates**		
date	day of the season (*date* = 1 is the earliest monitoring day of across all years), automatically incorporated into the required fields of the encounter history. Each day is 1 encounter occasion.	continuous
incubation day	incubation day (1–23) of a nest on any given day of monitoring	continuous
year	year of the study (2012–2015)	categorical
laydate	first egg laying date, coded as Julian date, enumerated from 1 January for each year	continuous
Land-use variables		
sheep density	mean density (inds. km^{-2}) extracted for 1 km radius buffers around nests from interpolated surface based on 4y data (low = 0–10 individuals km^{-2}, medium = 11–30 km^{-2}, high = 31–80 km^{-2})	continuous
Habitat variables		
shrub height	mean shrub height (cm) (n = 19 species) within 50 m	continuous
shrub frequency	total number of shrubs per composite sample (n = 19 species)	continuous
vegetation MDS1	nest-specific sample score from MDS analysis	continuous
vegetation MDS2	nest-specific sample score from MDS analysis	continuous
shrub assemblage	three shrub assemblages	categorical
topo.rugosity	standard deviation of elevation (m) per 30 m pixel within 100 m radius	

Potential effects of shrub composition were considered, separately examining continual measures and categorical ‘assemblages’. Local shrub species composition was summarised by two orthogonal ordination variables (*vegetation MDS1* and *vegetation MDS2*), provided by multidimensional scaling analysis (MDS) of the covariance matrix of composite shrub frequency data per sampling location (n = 871). Landscape-scale distribution of shrub assemblages (*shrub assemblage*) across the study area was classified and mapped, considering the eight most abundant shrub species (63.2% of all shrubs measured) using composite samples obtained from nests (n = 167) and an additional 704 sampling locations during May–June 2012, 2013 and 2014, with over 69,000 shrubs identified and recorded. Cluster analysis was performed on the Bray-Curtis similarity matrix of shrub frequencies (square-rooted), using average-linkage clustering and a 50% similarity level to select the most widespread assemblages (which classified 87% of all samples): (a) ‘*Artemisia*’ on gypseous/clay soils, dominated by *A. diffusa* (2,873 km^2); (b) ‘*Salsola rigida*’ on halophytic soils, dominated by *S. rigida* and *S. gemmascens* (2,180 km^2); (c) ‘*Salsola arbuscula*’ on gypseous and halophytic soils, dominated by *S. arbuscula*, with high density of *A. diffusa* and *S. rigida* (3,904 km^2); (d) ‘*Astragalus*’ on semi-consolidated sands, dominated by *A. villosissimus* and *Convolvulus hamadae*, also containing *Salsola* spp (3,778 km^2). A fifth, (e) ‘*Calligonum*’, on drifting or weakly consolidated sands and typified by *Calligonum* and *Salsola* spp. (1,603 km^2), was excluded from further consideration as no nests were found in this assemblage despite searches. Ordination and cluster analyses were performed in PRIMER 6.1.10 (Clarke 1993; Peet and Roberts 2013).

Topographic rugosity (*topo. rugosity*) was measured as the standard deviation of elevation within 100 m radius around nests (extracted from ASTER GDEM V2, 30 m horizontal resolution, 1 m vertical resolution).

Sheep were counted along 11,470 km of distance transects during 2012–2015, comprising 141 ten-kilometre off-road transects (with some repeated 2–3 times; total distance 3,500 km) driven in March–May 2012, and 1,594 five-kilometre transects each driven once along trackways or infrequently used roads in March–May 2013, 2014 and 2015. Average sampling intensity was 0.8 km transect per km^{-2} but relatively greater in higher sheep density areas, in order to capture local variability in distribution of sheep camps, and lower in remote areas with homogeneous low livestock density (Supplementary materials Fig. ESM5). For each sheep flock observed (total n = 938), the number of individuals (mean group size 159.9, *SD* ± 134.7, range 2–750) and distance to flock centre (measured by laser range-finder) were recorded. Preliminary year-specific distance analysis, with transect-specific sheep densities (allocated to transect centroids) interpolated to a density surface, showed that spatial distribution of livestock was strongly correlated and thus stable between years (Online resources, section 4; Table ESM2), as expected from the stable pattern of camp occupancy. We therefore created a composite sheep density surface (Fig. 1) by inverse distance-weighted averaging across all four years of transect-specific density estimates (n=1,735). In high to medium sheep density areas (within 20 km of the irrigation and settlement boundary) mean distance between camps proved to be 2.3 km (SD = 1.2); the close packing of sheep camps relative to greater sheep flock home ranges (~5 km around camps and wells; MK personal observations) suggest that grazing territories overlapped with all intervening desert subjected to grazing. We are therefore confident that interpolation of local sheep density measures is not obscuring or 'over-smoothing' local variation between grazed and undisturbed territories.

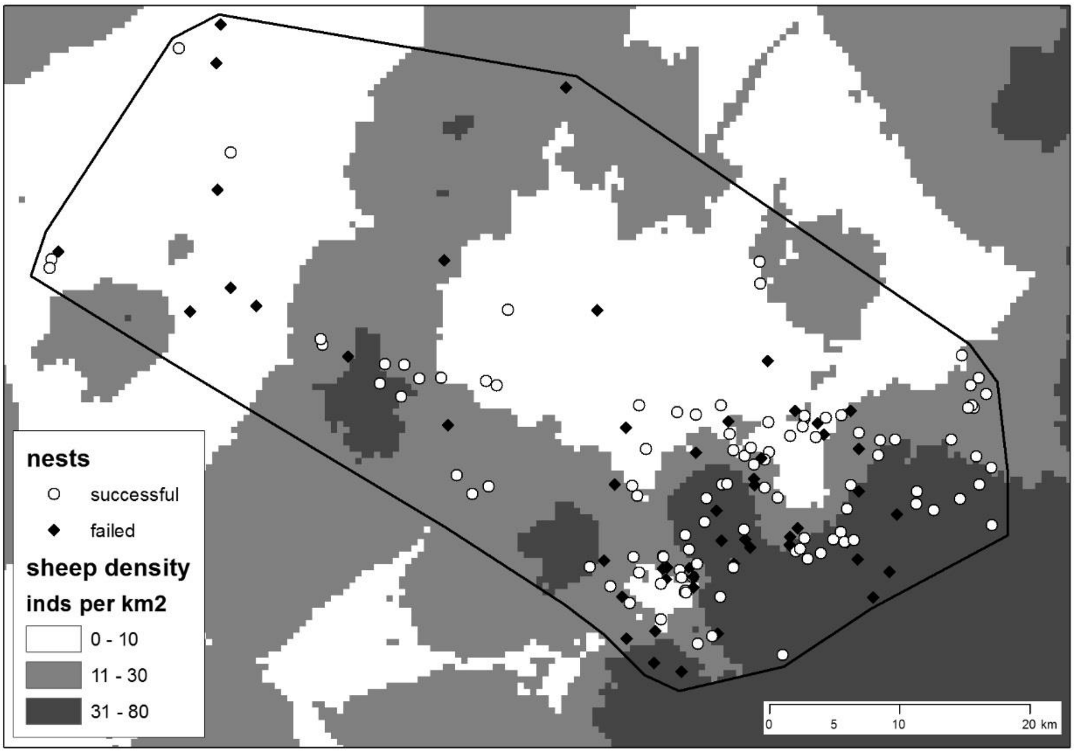

Figure 1. Distribution of wild Asian houbara nests across a gradient of sheep density monitored during four years of study within nest extent area (2,231 km^2) in southern Kyzylkum, Uzbekistan (excluding nests outside sampled territory and three nests found in *Artemisia* shrub assemblage).

Modelling effects of habitat and land-use on clutch size, nest success and hatchability

Clutch size and hatchability (number of eggs hatching within successful nests of known clutch size, with clutch size as an offset scaled with parameter 1.0) were examined using generalised linear models (GLMs) with Poisson error. Nest survival models were constructed in MARK (v 6.2), using the RMark package (Laake 2013) in R 3.1.1 (R Core Team 2013). Unlike the Mayfield method (Mayfield 1961) or its extension to logistic multivariate models (Aebischer 1999), modelling in RMark allows daily nest survival rate (dsr) to vary both with season and across incubation (Dinsmore et al. 2002). Mean probability of nest success per attempt, from the start of incubation to hatching (23 days), was estimated in RMark as the product of daily nest survival rates. Nests were considered as independent observations, since failure was considered to be largely stochastic (rather than related to female quality) and most were from different individuals. Laying dates are represented by Julian dates, enumerated from 1 January.

Nest success, clutch size and hatchability were *a priori* expected to vary among years, depending on conditions in wintering areas (carry-over effect) and on breeding grounds (e.g. variation in food availability, temperature and predator abundance). Additionally, likelihood of nest failure may change during the season (owing to increasing temperature and predator emergence) or with nest age (owing to accumulating female tracks and scent in later incubation or changes in duration or frequency of her absences from the nest). Therefore, for nest success potential effects of *year*, season (*date*) and its quadratic term ($date^2$) and *incubation day* were examined with GLMs inspecting change in AIC on variable removal. For clutch size and hatchability, potential effects of *year*, *laydate* and its quadratic term ($laydate+laydate^2$) were examined with similar GLMs. Strongly supported covariates (for which $\Delta AIC > +2.0$ on removal) were retained and forced into subsequent analysis of habitat and land-use effects (Table 1) in an information theoretic multi-model inference (MMI) framework, averaging across the full candidate model set (Burnham and Anderson 2002).

All candidate habitat and land-use variables were tested for inter-correlation (using either Pearson's or ANOVA) prior to modelling. *Vegetation MDS1* was related to both *shrub assemblage* (ANOVA, $F_{2,148} = 14.1$, $p = 0.001$; $R^2 = 0.14$) and *shrub height* (Pearson's $r = 0.52$). As *shrub height* received stronger support in univariate GLMs of nest success (on variable removal, $\Delta AIC = 5.1$) than *vegetation MDS1* ($\Delta AIC = -1.9$), the latter was excluded from subsequent analyses. However, *vegetation MDS2* (a continuous measure of shrub composition) was unrelated to *shrub height* (Pearson's $r = -0.07$) and so was included in model sets with this measure of vegetation structure. Lastly, categorical *shrub assemblage* was examined in an alternative model set that did not include vegetation structure, as it was correlated with *shrub height* (ANOVA, $F_{2,148} = 25.1$, $p = 0.001$; $R^2 = 0.24$).

Monitoring nests using nest-cameras may potentially bias overall nest success and information on the relative importance of predator species, as cameras may affect species-specific predation rates (Richardson et al. 2009). Camera deployment on nests was opportunistic, often not spanning the entire nest monitoring period. Therefore, to test for any potential influence of nest-cameras on nest survival, exposure days for nests monitored in 2014 and 2015 (years in which cameras were used) were partitioned between days with and without camera, coding days preceding camera deployment as successful, running univariate models in MARK, controlling for year and inspecting ΔAIC on variable removal.

MMI was applied to all models using the MuMIn package in R (Barton 2013) to estimate model-averaged coefficients and unconditional standard errors accounting for the Akaike weight of each candidate model (Burnham and Anderson 2002). The apparent degree of support for effects may be inflated by reliance on relative variable importance (RVI) (the sum of Akaike weights of all models in which the variable occurs) when there are many competing models (Boughey et al. 2011). Therefore, we examined also the 95% null interval of the probability distribution of RVI for a random variable (mean = 1, SD = 1) across 1,000 MMI iterations, following Boughey et al. (2011). Support for a predictor was further assessed by inspecting the 95% unconditional confidence intervals of averaged parameter coefficients. Effects were considered strongly supported when model-averaged parameter estimates lay beyond the 95% null interval and 95% parameter CIs did not span zero. Data were not over-dispersed, as the ratio of residual deviance to residual degrees of freedom (Crawley 2007) was <1.0 for all three full models.

Results

Temporal and spatial distribution of nests

Earliest laying dates varied among years (range 14–24 March) with the latest clutch initiated on 15 May in 2015; however, the median laying date was remarkably consistent for three years (2, 1 and 2 April, for 2012, 2013 and 2014 respectively), although slightly later (8 April) in 2015. For 10 satellite-tagged females, 15 first nesting attempts were started a mean of 12.6 (range 8–20) days after arrival in the breeding area. Females started laying only after daily minimum temperatures consistently exceeded 0 ℃, and laying generally ceased once maximum daily temperatures consistently exceeded 25 ℃ (usually in early May; see Online resources, Fig.ESM1).

Nests were mainly found in areas dominated by semi-consolidated and loose sand owing to greater ease of tracking. Consequently, only 16 nests (9.0% of all nests) were found within areas dominated by clay substrates (over 75% clay coverage, estimated over four replicate 2 m x 2 m quadrats placed 50 m from the nest) (Supplementary materials, Fig. ESM4), involving either satellite-tagged females (nine nests), flushing a female near a nest (two nests), watching a female return to a nest (one nest) or tracking (four nests).

Of those nests in the core study area for which livestock density was mapped, most were found in areas with medium (n = 69) density, with fewer in areas of high (n = 45) or low (n = 41) density. Relative to area, fewer nests were found in areas of low livestock density ($\chi^2_3 = 12.3, p = 0.01$) (Online resources, Fig. ESM2), probably owing to reduced search effort in remote areas. Nests were located within vegetation of varying shrub frequency (mean ± SD = 64.2 ± 28.8 shrubs/200 m, range = 15–151) and height (mean ± SD = 31.2 ± 8.1 cm, range = 12.7–67.3).

Clutch size

Preliminary GLMs showed no support for effects on clutch size of season (removal of *laydate*^{2} and then *laydate*: $\Delta AIC = -1.7$ and -0.8 respectively) or *year* ($\Delta AIC = -3.4$), so neither *laydate* nor *year* was included in MMI. Clutch size was not affected by any habitat or land-use variables (Fig.2a). Here we present results for MMI that incorporated *vegetation MDS2* and *shrub height* (both continuous); however, similar results were obtained with an alternative set of models that considered the categorical variable *shrub assemblage*. Clutch size (mean ± SD = 3.2 ± 0.6 eggs; range 2–5) was similar among areas with different sheep density (low, mean ± SE = 3.4 ± 0.1 eggs; medium, 3.3 ± 0.1 eggs; high, 3.1 ± 0.1 eggs; *ΔAIC* = –1.8) and shrub assemblages (*S. rigida*, mean ± SE = 3.0 ± 0.1 eggs; *S.arbuscula*, mean ± SE = 3.3 ± 0.1 eggs; *Astragalus*, mean ± SE = 3.2 ± 0.1 eggs; *ΔAIC* = –2.6). Egg volume decreased by approximately 5% (change between first and last date quartiles as % of mean) with laydate (β = 0.0003, SE ± 0.00007; *ΔAIC* = 5.0; GLMM with gamma error, controlling for nest ID as random effect), but did not differ between years (*ΔAIC* = –3.0; GLMM with gamma error, nest ID as random effect).

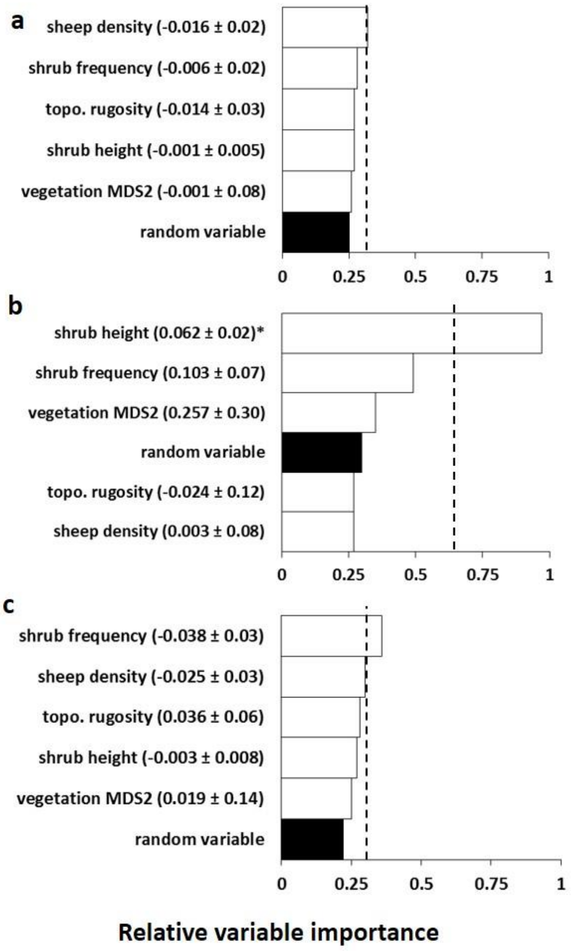

Figure 2. Relative variable importance (RVI: sum of AIC weights) and model-averaged coefficient ± unconditional SE of predictors (in parentheses) from multi-model inference of (a) clutch size, (b) nesting success and (c) hatchability (the proportion of eggs hatching within a successful nest) of Asian houbara *Chlamydotis macqueenii* in the Kyzylkum Desert, Uzbekistan. Parameter estimates for individual levels within categorical variables (*shrub assemblage* and *year*) are not shown. (*) denotes strongly supported predictors (averaged parameter estimate CIs not spanning zero and RVI beyond 95% null limit). For each set of models, the median RVI (filled box) and upper 95% null limit (dashed line) of a randomly generated predictor are shown (see text for details).

Nest success

Nest success was estimated from 163 nests with 1,913 exposure days, excluding 14 nests with unknown outcome or zero exposure days (found at hatching or at predation). Mean nest success across four years was 51.4% (95% CI, 42.4–60.4%). There was no evidence of any effect of nest-camera on dsr (ΔAIC = –1.7 on variable removal), with similar rates for nests with (97.7%; n = 35 nests; 429 exposure days) and without cameras (97.0%; n = 61 nests; 683 exposure days). Further *a priori* modelling showed daily survival rate did not vary between years (Fig. 3) and did not decline with *incubation day* (ΔAIC = –2.0 and –1.8 on removal of *year* and *incubation day* respectively). However, there was strong support for a quadratic relationship between nest success and day of season (ΔAIC = 2.4 and 0.7 on removal of $date^2$ and then *date* respectively), with higher survival early in the season (1st week mean ± SE = 74.9% ± 7.0%), decreasing by around 50% by 4th week (mean ± SE = 37.1% ± 7.0%) and then slightly increasing towards the end (6th week mean ± SE = 44.7% ± 14.1%) (Fig. 4); therefore *date* + $date^2$ were forced into MMI. Modelling of solely the first three years again supported the linear effect of *date* (ΔAIC = 2.1 on variable removal), but the quadratic effect of $date^2$ on daily nest survival was only important when nests from 2015 were included in the analysis, potentially owing to an extended season and later nests in that year.

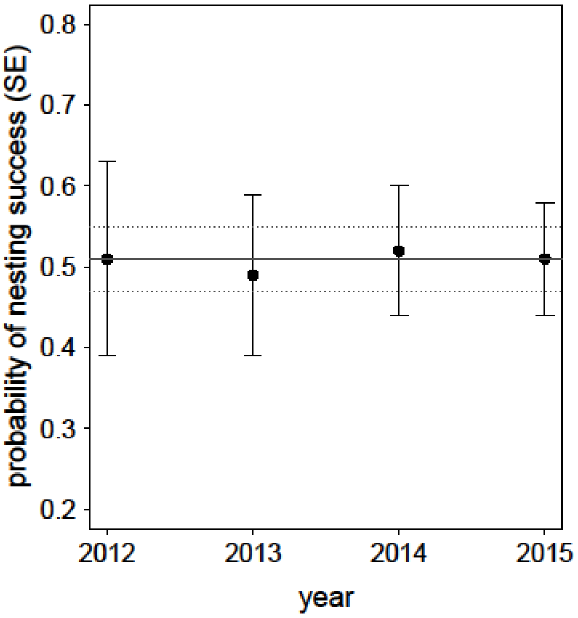

Figure 3. Inter-annual variation of nest success in Asian houbara *Chlamydotis macqueenii* in the Kyzylkum Desert, Uzbekistan (vertical bars show standard error, horizontal line represents mean nesting success across four years, dotted lines are SE of the mean).

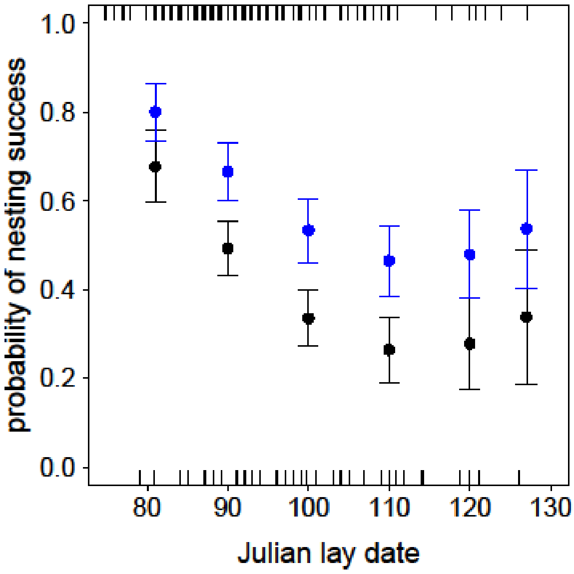

Figure 4. Estimated variation of nest hatching success (vertical bars are SEs) with the additive effects of first egg lay date and mean shrub height around the nest (50 m radius) for Asian houbara *Chlamydotis macqueenii* in the Kyzylkum Desert, Uzbekistan. Blue dots are the upper, 35.8 cm, and black are the lower, 26.5 cm, quartiles of the shrub height distribution. Observed outcomes are shown as jitter on the top and bottom axes, where 0 is failed to hatch and 1 is hatched. Julian lay date is number of days from 1 January.

Predation represented 85% of failures for which the cause was known, with the predator responsible identified or inferred in 73% of predated nests, including desert monitor (*Varanus griseus;* n = 26) and fox (*Vulpes vulpes* or *V. corsac*; n = 4). Nests were more susceptible to desert monitor predation later in the season, when tested in univariate models in RMark (coding outcome as: 1 = desert monitor predation, 0 = success or another cause of failure; ΔAIC = 9.5, ΔAIC = 3.6 on removal of $date^2$ and then *date* respectively). Similarly, the probability of nest failure from other causes changed through the season, but only the quadratic term of *date* was supported (outcome as: 1 = all causes of failure other than desert monitor, 0 = success or desert monitor predation, $date^2$: ΔAIC = 3.1, *date*: ΔAIC = –2.0). Two clutches were apparently taken by shepherds, three were trampled by sheep and two held undeveloped eggs (Table 2).

Table 2. Causes of nest failure and number of successful nests for Asian houbara *Chlamydotis macqueenii* in the Kyzylkum Desert, Uzbekistan; n = 174 nests with known outcome monitored during 2012–2015, separately for nests laid before and after the median laying date (2 April).

	before median	**after median**	**Total**
successful nests	58	57	115
causes of nest failure			
total failed	18	41	59
desert monitor	6	20	26
fox sp.	1	3	4
unconfirmed predator	2	9	11
shepherd	1	1	2
trampled by sheep	3	0	3
failed to hatch	0	2	2
failed (reason unknown)	5	6	11

Video in 2014 recorded sheep flocks in the proximity on 24 occasions at five of nine nests, with females leaving when sheep approached in 11/24 instances, yielding a mean disturbance rate at these nests of 0.12 day^{-1} (SE ± 0.03) and across the nine nests of 0.09 day^{-1} (SE ± 0.02) (Online resources, section 3). Females appeared to stay off the nest longer (ΔAIC = 18.8 on variable removal, controlling for nest ID as random effect) after sheep disturbance (n = 11, mean ± SD = 46.2 ± 26.2 minutes) than after other absences for the same five nests (n = 296, mean ± SD = 22.1 ± 25.0 minutes), possibly because sheep flocks take some time to pass through an area.

Probability of houbara nesting success was substantially greater (mean ± SE = 65.5% ± 6.5%) with taller mean shrub height (upper quartile mean = 35.8 cm) than with lower mean shrub height (lower quartile mean = 26.4 cm; mean nesting success ± SE = 47.3% ± 6.0%), the effect being strongly supported with an RVI well beyond the 95% null interval and CIs not spanning zero (Fig.2b, Fig.4). In contrast, nest success was not affected by sheep density, topographic rugosity, shrub density or shrub composition (i.e vegetation MDS2), with CIs spanning zero and RVIs within 95% null interval (Fig.2b). The alternative MMI incorporating *shrub assemblage,* instead of *shrub height*, showed no support for any of the predictors modelled.

Hatchability

Hatchability was high, with 87.5% (95% CI, 83.1–91.8%) probability of an egg in a successful nest hatching (n = 196 chicks hatched from 224 eggs; n = 68 nests suitable for analysis). Controlling for female ID as a random effect in univariate tests indicated no support for an effect of $laydate^2$ ($\Delta AIC = 0.3$) or *laydate* ($\Delta AIC = 1.6$) on hatchability, so *laydate* was not included in MMI as a candidate effect. No support for influence of any land-use or habitat variables on hatchability (and thus embryo survival) was found (CIs spanning zero; RVI within 95% null interval) (Fig.2c), with alternative MMI models incorporating *shrub assemblage* giving similar results.

Discussion

Asian houbara nest productivity did not vary between three shrub assemblages or with moderate levels of pastoralism activity and infrastructure, but nests placed within taller vegetation experienced greater success. Daily nest survival decreased with season, probably owing to the emergence of monitor lizards, but also showed some recovery at the end of the nesting season, perhaps as activity of this predator declined. Mean nest success of 51.4% (95% CI, 42.4–60.4%), estimated from 163 nests over four years, was similar to a three-year mean from China (mean = 58.8 %, SD = 27.0, n = 45; Combreau et al. 2002) and a five-year study in Israel (mean = 47%, n = 12; Lavee 1988). We are unable to compare this level of nest success to that of other bustard species owing to a lack of similar reliable data on these cryptic birds.

Nest predation

Predation was the main cause of nest failure, accounting for at least 70% of all failed nests and 85% of those for which the cause was considered known. In contrast, removal of eggs by shepherds or trampling by sheep accounted for 11% of all nest failures and for 10% of those where the cause was known, and sheep density had no detectable effect on nest success. Predation by desert monitors contributed 54% of all nest failures for which the cause was considered known and 63% of known predation. Although predation of houbara nests by this species has been noted previously (Gubin 2004; Launay et al. 1997), predation by foxes and corvids is reported more frequently (Combreau and Launay 1999; Combreau et al. 2002; Gubin 2004; Lavee 1988). In our study, only 10% of known predation was attributable to foxes and, even assuming that foxes may have contributed disproportionately to nests affected by 'unknown' predators (a further 27% of known predation), monitors remain the primary nest predator. However, low rodent abundance throughout this study may have depressed fox numbers.

Species responsible for nest predation were mostly inferred from tracks and signs, except for 10 predations by desert monitors recorded on nest-cameras. Desert monitors often left claw/tail marks and either emptied the nest (if all eggs were swallowed unbroken) or left some yolk and eggshell fragments (if eggs broke during swallowing). Foxes, in contrast, are unlikely to leave many tracks by the nest and often carry the eggs away to eat or hide, so there may be no remains close to the scrape (MK pers. obs.; Combreau et al. 2002). Foxes were probably responsible for some of the unattributed nest predation (Online resources, section 3); however, even if all unattributed predation and all unknown-cause failures were attributed to foxes (inevitably a considerable over-estimate) predation by foxes would still be below that by desert monitors (37.2% and 44.1% of all failures, respectively).

In contrast to the lack of inter-annual variation in nest success in our study, in China large variation between years was attributed to fluctuation in predator densities (Combreau et al. 2002). Such variability is expected in regions where populations of rodents such as great gerbil *Rhombomys opimus* (a staple prey of Central Asian mammalian predators) exhibit pronounced temporal fluctuations (Gauthier et al. 2004; Linné Kausrud et al. 2007; Salek et al. 2004). Rodent numbers (particularly gerbils) fluctuate in Bukhara (Shenbrot and Rogovin 1995), but following a peak in 2010 the abundance of both rodents and mammalian carnivores remained low in all four study years (MK unpubl. data). However, the substantial contribution of monitors to nest predation may dampen any inter-annual variation in nest productivity arising from future changes in fox numbers following rodent outbreak years.

Predator control is often advocated as a conservation measure for vulnerable bird species, and can enhance both breeding productivity and subsequent population size (Smith et al. 2010). However, sustained removal of predators poses both ethical and practical problems. Landscape-scale extirpation or substantial suppression of desert monitor numbers may have potential unforeseen effects, e.g. increasing rodent prey and thus generalist predator numbers. Moreover, the species is persecuted widely for use in traditional medicine and has an unfavourable conservation status in several countries

(Bergin and Nijman 2014; Grigoryants 2010; Kovshar 1996). We oppose the control of desert monitors as a measure to increase houbara numbers.

Effect of season

Early clutches had higher chances of survival owing to the later emergence of desert monitors (n = 58 monitor observations, first date = 15 April, median date = 13 May), with chances of nest success decreasing by almost 50% by the end of the season, coinciding with peak of monitor activity in May–June (Pianka et al. 2004). As the number of active nests diminishes towards the end of the breeding period, finding new nests by tracking becomes extremely difficult, with smaller sample sizes in the first three years of study limiting our ability to detect any increase in late-season nest survival. However, in 2015 substantially more late-season nests were found (mostly nests of PTT-tagged females), increasing sample size sufficiently to detect a subsequent (approx. 7%) partial recovery in nest survival, potentially attributable to seasonal phenology of monitors.

Habitat effects

Higher nest success in areas with taller mean shrub vegetation (mean height ± SD = 32.6 ± 8.2 cm and 29.1 ± 7.4 cm for successful and failed nests respectively; Fig.4) suggests that females may benefit from concealment by shrubs. Incubating females often react to an approaching threat by running away fast, keeping head and neck low (observations from nest-cameras). In slightly taller vegetation these large birds may have a greater chance of fleeing the nest undetected by a predator, analogous to the concealment effect of small-scale topographic rugosity for nesting great bustard *Otis tarda* (Magana et al. 2010). We found no effect of topographic rugosity on houbara nest success, perhaps because this relatively coarse measure (30 m horizontal resolution, examined over a radius of 100 m) failed to capture smaller-scale topographic cover near nests. Another explanation is that hillocks and elevations probably do not provide much additional concealment against major predators for incubating females. Foxes, being mostly nocturnal, rely on smell or sound when foraging, while in shrubby desert diurnal monitor lizards, although thought to have excellent vision like other *Varanus* (Pianka et al. 2004), seem more likely to detect a nest or a female at relatively close range, so nesting in a depression between hillocks or in a flat area may have similar costs for nest survival.

We found no difference in nest success, clutch size or hatchability between the three shrub assemblages considered. In contrast, male abundance within the same study area varied between these assemblages (MK unpubl. data), being substantially higher in *Salsola rigida* than in *Salsola arbuscula* and *Astragalus* habitats. Higher male numbers in *Salsola rigida* habitat are likely to be related to better conditions for display visibility over large distances in this flatter habitat, dominated by short and dwarf shrubs. For the habitats assessed here it seems that, as long as females can find localised areas with suitable taller shrubs to camouflage their movements, nests have greater chance of success irrespective of shrub species composition. Breeding male houbara, by contrast, occur in higher abundances where vegetation is shorter (Koshkin et al. 2014; Koshkin et al. in press), indicating the importance of landscape heterogeneity for the species. Such variation is provided by local topographical relief within each of the widely distributed plant assemblages studied here.

Although few nests were found in areas where clay substrate dominated, we attribute this to difficulties tracking on these substrates and do not infer a difference in habitat preference or densities of nesting females. Moreover, male densities in some clay areas were found to be higher than in areas with consolidated sand (Koshkin et al. in press), which suggests high local availability of breeding females; densities of main predators do not seem to depend on substrate (pers. obs.). We therefore have no reason to expect a lower density of nesting females in clay-dominated areas.

Land-use effects

Absence of any detectable effects of livestock density on houbara nest success or hatchability in successful nests agrees with Johnson et al. (2012), who found no effect of different stocking rates and only a minor effect of trampling on nest success for a range of ground-nesting passerine species in dry savanna in Oregon, USA. However, in Israel high densities of livestock (at mean density of 80 individuals km^{-2}) were considered the main cause of poor nest success in Asian houbara (Lavee 1988), based on observations of sheep flocks displacing incubating females from nests, potentially exposing eggs to unfavourable temperatures and predation. Contrasts may arise due to differences in grazing systems among regions, including density, seasonality and duration of grazing, as well as cultural factors (e.g. dog use, egg-collection and subsistence hunting by shepherds). We also acknowledge lack of samples of nests from areas with the most extreme (> 80 individuals km^{-2}) sheep density where we failed to locate any nests, owing to difficulties in tracking over sand heavily disturbed by sheep and also perhaps to lower nesting densities there. Human nest-robbing appears to be a minor factor in the Kyzylkum.

Video monitoring of a sample of nests disturbed at least once by sheep flocks (often accompanied by shepherds) suggested that displacement rates were low even for this subset of nests. Nevertheless, females were absent for twice as long compared to other causes (displaced by cars, other houbara or unknown reasons) (Online resources, section 3), potentially exposing clutches to predators and uncontrolled temperatures for longer periods. This and the fact that all three nests trampled in our study were located in areas of high sheep density (> 50 individuals km^{-2}) suggest that extreme livestock densities could indeed compromise houbara nest success. Further telemetry data may reveal whether nesting females avoid very high sheep densities when selecting nest sites, as presence of sheep flocks prior to houbara arrival provides a potential cue for settlement.

Implications and further research

Nesting success was unaffected by variation in shrub species composition or livestock density, suggesting that the Asian houbara is a versatile, adaptable occupant of a range of arid habitats.

Initiation of clutches within one or two weeks of return to the Kyzylkum, at a time when weather conditions are generally wintry, desert plants still dormant and evidence of invertebrate life hard to find (pers. obs.), indicates that females retain significant reserves after their migration. This quick onset of breeding may be a strategy to avoid incubation during the period of peak monitor activity, when nest success suffers a 50% reduction, but females may also be under pressure to complete nesting well ahead of maximum summer temperatures (July–August), so that chicks optimise benefits from the spring flush (May–June) of resource availability (Daan et al. 1989). Lack of difference in egg volume between years is in contrast to the observed difference in chick weight (Burnside, unpubl. data), suggesting that egg productivity depends on resources in wintering or passage sites, rather than foraging conditions on the breeding grounds. Conditions and habitat suitability in wintering and staging areas may therefore have important carry-over effects for productivity as well as for winter survival.

We found no difference in houbara clutch size or nest success among habitats and with different livestock densities. In theory, for species with non-exclusive home ranges ideal free settlement could allow compensatory density-dependence, masking underlying differences in habitat quality and productivity (Dolman 2012), but we cannot envisage a mechanism for strong density-dependent houbara breeding productivity. Prey depletion is unlikely at the scale of female home range, and predator aggregation in response to landscape-scale variation in houbara density is unlikely. Consequently, we consider that this range of habitats provides a broadly similar quality for nesting females. The protection of extensive halophytic landscapes is therefore required. The similar levels of nest productivity in *Salsola arbuscula*, *S.rigida* and *Astragalus* habitats suggest that all three are key and should be protected against further habitat loss or infrastructure development (pipelines, powerlines, roads). Although we were unable to examine nest success in *Calligonum* habitat, few houbara are encountered in this habitat during the breeding season (Gubin 2004; Koshkin et al. 2014). The role of *Artemisia*-dominated habitat, insufficiently sampled in this study, needs further examination. Although we found no differences in nest productivity, we did not test whether rates of juvenile survival (which also contribute to overall breeding productivity) differ between habitats.

Our results suggest that Asian houbara in the southern Kyzylkum have good nest success while tolerating current levels of sheep grazing and human disturbance. As nesting productivity was similar across habitat and land-use gradients, this study provides no obvious mechanisms to enhance natural productivity. Therefore the minimisation of anthropogenic mortality during migration and winter—with offtake regulated under a quota system and additive mortality reduced across an extensive migratory corridor—remains the most immediate solution for securing the future of the species and rendering hunting sustainable in the long term.

Acknowledgements

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References

Aebischer NJ (1999) Multi-way comparisons and generalized linear models of nest success: Extensions of the Mayfield method. Bird Stud 46:S22-S31

Aghanajafizadeh S, Hemami MR, Heydari F (2012) Nest-site selection by the Asian Houbara Bustard, *Chlamydotis macqueenii*, in the steppe of Harat, Iran (Aves: Otidae). Zool Middle East 57:11-18 doi:Doi 10.1080/09397140.2012.10648958

Barton K (2013) MuMIn: multi-model inference. R package version 1.15.1, URL http://cran.r-project.org/web/packages/MuMIn/index.html.

Bergin D, Nijman V (2014) Open, unregulated trade in wildlife in Morocco's markets. TRAFFIC Bulletin 26:65-70

BirdLife International (2015) Species factsheet: *Chlamydotis macqueenii*. Downloaded from http://www.birdlife.org on 22/08/2015.

Boughey KL, Lake IR, Haysom KA, Dolman PM (2011) Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. Biol Conserv 144:2300-2310 doi:10.1016/j.biocon.2011.06.008

Burnham KP, Anderson DR (eds) (2002) Model selection and multi-model inference. A practical information-theoretic approach. Springer, New York

Burnside RJ, Collar NJ, Scotland KM, Dolman PM (in press) Survival rates of captive-bred Asian Houbara *Chlamydotis macqueenii* in a hunted migratory population. Ibis

Carrascal LM, Palomino D, Seoane J, Alonso CL (2008) Habitat use and population density of the houbara bustard *Chlamydotis undulata* in Fuerteventura (Canary Islands). Afr J Ecol 46:291-302 doi:10.1111/j.1365-2028.2008.00971.x

Chargé R, Sorci G, Saint Jalme M, Lesobre L, Hingrat Y, Lacroix F, Teplitsky C (2014) Does recognized genetic management in supportive breeding prevent genetic changes in life-history traits? Evol Applic 7:521-532 doi:10.1111/eva.12150

Clarke KR (1993) Nonparametric multivariate analyses of change in community structure. Aust J Ecol 18:117-143 doi:10.1111/j.1442-9993.1993.tb00438.x

Combreau O, Launay F (1999) An estimation of the nesting success in a Houbara Bustard *Chlamydotis undulata macqueenii* population in Kazakhstan. Sandgrouse 21:171-175

Combreau O, Qiao J, Lawrence M, Gao X, Yao J, Yang W, Launay F (2002) Breeding success in a Houbara Bustard *Chlamydotis* [*undulata*] *macqueenii* population on the eastern fringe of the Jungar Basin, People's Republic of China. Ibis 144:E45-E56 doi:DOI 10.1046/j.1474-919X.2002.00054.x

Crawley MJ (2007) The R book. Wiley Publishing,

Daan S, Dijkstra C, Drent R, Meijer T (1989) Food supply and the annual timing of avian reproduction. In: Acta XIX Congr. Int. Omithol., Ottawa. pp 392-407

Dinsmore SJ, White GC, Knopf FL (2002) Advanced techniques for modelling avian nest survival. Ecology 83:3476-3488 doi:10.1890/0012-9658(2002)083[3476:atfman]2.0.co;2

Dolman PM (2012) Mechanisms and processes underlying landscape structure effects on bird populations. In: Fuller RJ (ed) Birds and Habitat: Relationships in Changing Landscapes. Cambridge University Press, Cambridge

Dolman PM, Collar NJ, Scotland KM, Burnside RJ (2015) Ark or park: the need to predict relative effectiveness of *ex situ* and *in situ* conservation before attempting captive breeding. J Appl Ecol 52:841-850 doi:10.1111/1365-2664.12449

Frankham R (2008) Genetic adaptation to captivity in species conservation programs. Mol Ecol 17:325-333 doi:10.1111/j.1365-294X.2007.03399.x

Gauthier G, Bêty J, Giroux J-F, Rochefort L (2004) Trophic interactions in a high Arctic Snow Goose colony. Integr Comp Biol 44:119-129 doi:10.1093/icb/44.2.119

Gintzburger G, Toderich KN, Mardonov BK, Mahmudov MM (2003) Rangelands of the arid and semi-arid zones in Uzbekistan. CIRAD, ICARDA, Paris

Grigoryants AA (ed) (2010) Red data book of Uzbekistan vol 2. Chinor ENK, Tashkent

Gubin BM (2004) Drofa-krasotka (Houbara Bustard) (in Russian). Kolor, Almaty

Hardouin LA, Hingrat Y, Nevoux M, Lacroix F, & Robert A. (2015) Survival and movement of translocated houbara bustards in a mixed conservation area. Animal Conservation, 18(5), 461-470. doi:10.1111/acv.12196

Hingrat Y, Saint Jalme M, Chalah T, Orhant N, Lacroix F (2008) Environmental and social constraints on breeding site selection. Does the exploded-lek and hotspot model apply to the Houbara bustard *Chlamydotis undulata undulata*? J Avian Biol 39:393-404 doi:10.1111/j.2008.0908-8857.03994.x

Hoyt DF (1979) Practical methods of estimating volume and fresh weight of birds' eggs. Auk 96:73-77

Islam MZ, Basheer MP, Shah MS, al Subai H, Boug A (2012) Captive-breeding and reintroduction of the Asian Houbara Bustard *Chlamydotis macqueenii* in the Kingdom of Saudi Arabia: lessons learned. Internat Zoo News 59:338-360

Johnson TN, Kennedy PL, Etterson MA (2012) Nest success and cause-specific nest failure of grassland passerines breeding in prairie grazed by livestock. J Wildl Manage 76:1607-1616 doi:10.1002/jwmg.437

Kerven C, Shanbaev K, Alimaev J, Smailov A, Smailov K (2006) Livestock mobility and degradation in Kazakhstan's semi-arid rangelands. In: Behnke R (ed) Socio-economic causes and consequences of desertification in Central Asia. Nato Science for Peace and Security Series C - Environmental Security. Springer, Dordrecht, pp 113-140. doi:10.1007/978-1-4020-8544-4_6

Koshkin MA, Collar NJ, Dolman PM (2014) Do sheep affect distribution and habitat of Asian Houbara *Chlamydotis macqueenii*? J Arid Environ 103:53-62 doi:10.1016/j.jaridenv.2014.01.002

Koshkin MA, Burnside RJ, Collar NJ, Guilherme JL, Showler DA, Dolman PM (in press) Effects of habitat and land-use on breeding-season density of male Asian Houbara *Chlamydotis macqueenii*. J Ornithol

Kovshar AF (ed) (1996) Red data book of Kazakhstan. Almaty

RMark: An R interface for analysis of capture-recapture data with MARK (2013) AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

Launay F, Loughland R, Mukhina EA (1997) Preliminary observations of the incubation and covey behaviour of Houbara Bustard *Chlamydotis undulata macqueeni*. Sandgrouse 19:51-55

Lavee D (1988) Why is the Houbara *Chlamydotis undulata macqueenii* still an endangered species in Israel? Biol Conserv 45:47-54

Le Cuziat J, Lacroix F, Roche P, Vidal E, Medail F, Orhant N, Beranger PM (2005a) Landscape and human influences on the distribution of the endangered North African houbara bustard (*Chlamydotis undulata undulata*) in Eastern Morocco. Anim Conserv 8:143-152 doi:10.1017/s1367943005001903

Le Cuziat J, Vidal E, Roche P, Lacroix F (2005b) Human activities affect the potential distribution of the Houbara Bustard *Chlamydotis undulata undulata*. Ardeola 52:21-30

Linné Kausrud K et al. (2007) Climatically driven synchrony of gerbil populations allows large-scale plague outbreaks. P Roy Soc B-Biol Sci 274:1963-1969 doi:10.1098/rspb.2007.0568

Magana M, Alonso JC, Martin CA, Bautista LM, Martin B (2010) Nest-site selection by Great Bustards *Otis tarda* suggests a trade-off between concealment and visibility. Ibis 152:77-89 doi:10.1111/j.1474-919X.2009.00976.x

Mallord JW, Dolman PM, Brown A, Sutherland WJ (2007) Nest-site characteristics of Woodlarks *Lullula arborea* breeding on heathlands in southern England: are there consequences for nest survival and productivity? Bird Stud 54:307-314 doi:10.1080/00063650709461490

Mayfield H (1961) Nesting success calculated from exposure. Wilson Bull 73:255-261

Mayfield H (1975) Suggestions for calculating nesting success. Wilson Bull 87:456-466

O'Brien M, Green RE, Wilson J (2006) Partial recovery of the population of Corncrakes *Crex crex* in Britain, 1993–2004. Bird Stud 53:213-224 doi:10.1080/00063650609461436

Peet RK, Roberts DW (2013) Classification of natural and semi-natural vegetation. In: Vegetation ecology. John Wiley & Sons, Ltd, pp 28-70. doi:10.1002/9781118452592.ch2

Perrins CM, Lebreton J-D, Hirons GJM (eds) (1993) Bird population studies: relevance to conservation and management. Oxford University Press, Oxford

Pianka ER, King D, KIng RA (eds) (2004) Varanoid lizzards of the world. Indiana University Press, Bloomington, Indiana

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, URL http://www.R-project.org/. Vienna, Austria

Richardson TW, Gardali T, Jenkins SH (2009) Review and meta-analysis of camera effects on avian nest success. J Wildl Manage 73:287-293 doi:10.2193/2007-566

Riou S, Judas J, Lawrence M, Pole S, Combreau O (2011) A 10-year assessment of Asian Houbara Bustard populations: trends in Kazakhstan reveal important regional differences. Bird Conserv Int 21:134-141 doi:10.1017/s0959270910000377

Robinson RA, Green RE, Baillie SR, Peach WJ, Thomson DL (2004) Demographic mechanisms of the population decline of the song thrush *Turdus philomelos* in Britain. J Anim Ecol 73:670-682 doi:10.1111/j.0021-8790.2004.00841.x

Robinson TP, Franceschini G, Wint W (2007) The Food and Agriculture Organization's gridded livestock of the world. Vet Ital 43:745-751

Salek M, Svobodova J, Bejcek V, Albrecht T (2004) Predation on artificial nests in relation to the numbers of small mammals in the Krusne hory Mts, the Czech Republic. Folia Zool 53:312-318

Shenbrot GI, Rogovin KA (1995) Temporal variation in spatial organization of a rodent community in the southwestern Kyzylkum desert (Middle Asia). Ecography 18:370-383 doi:10.1111/j.1600-0587.1995.tb00140.x

Smith RK, Pullin AS, Stewart GB, Sutherland WJ (2010) Effectiveness of predator removal for enhancing bird populations. Conserv Biol 24:820-829 doi:10.1111/j.1523-1739.2009.01421.x

Snyder NFR, Derrickson SR, Beissinger SR, Wiley JW, Smith TB, Toone WD, Miller B (1996) Limitations of captive breeding in endangered species recovery. Conserv Biol 10:338-348 doi:10.1046/j.1523-1739.1996.10020338.x

Sutherland WJ, Newton I, Green RE (2004) Bird ecology and conservation: a handbook of techniques. Oxford University Press, Oxford

Tourenq C et al. (2005) Alarming houbara bustard population trends in Asia. Biol Conserv 121:1-8 doi:10.1016/j.biocon.2004.03.031

Waber K, Spencer J, Dolman PM (2013) Achieving landscape-scale deer management for biodiversity conservation: the need to consider sources and sinks. J Wildl Manage 77:726-736 doi:10.1002/jwmg.530

Williams SE, Hoffman EA (2009) Minimizing genetic adaptation in captive breeding programs: a review. Biol Conserv 142:2388-2400 doi: http://dx.doi.org/10.1016/j.biocon.2009.05.034

Wright LJ, Hoblyn RA, Green RE, Bowden CGR, Mallord JW, Sutherland WJ, Dolman PM (2009) Importance of climatic and environmental change in the demography of a multi-brooded passerine, the woodlark *Lullula arborea*. J Anim Ecol 78:1191-1202 doi:10.1111/j.1365-2656.2009.01582.x

Yang WK, Qiao JF, Combreau O, Gao XY, Zhong WQ (2003) Breeding habitat selection by the Houbara Bustard *Chlamydotis [undulata] macqueenii* in Mori, Xinjiang, China. Zool Stud 42:470-475

Chapter 4 – Supplementary materials (Online resources)

Section 1. Nest monitoring

It is important to minimise potential bias related to nest visits, particularly as disturbance, frequent visits or scent may potentially affect subsequent rates of nest predation (Thompson III et al. 1999) or have positive effects on nest survival by deterring predators (Ibáñez-Álamo et al. 2012; Ibáñez-Álamo and Soler 2010). Nesting in open habitat and vulnerable to predation by fox (*Vulpes vulpes*, though potentially also *V. corsac*), scent is a particular consideration when monitoring houbara nests (Combreau et al. 2002). In 2012, eggs were not measured and laying date was estimated from hatching date, with a range of uncertainty calculated for those nests that failed according to monitoring duration and incubation period, following Mallord et al. (2007). In 2013, 2014 and 2015, when a nest was first found clutch size was recorded and eggs were weighed using an electronic scale with 0.1g accuracy and the maximum width and length measured using dial callipers with 0.1mm accuracy, while handled with fresh latex gloves to prevent transfer of scent or bacteria. Fieldworkers approached nests carefully and did not kneel at nests, to minimise scent or sign and the nest area was left using the same route which was swept (using local vegetation) to remove footprints. Location of each nest was recorded using handheld GPS and marked with an unobtrusive marker, set >10 m away from a nest, recording a bearing from the marker to the nest. It took five to ten minutes, starting from finding the nest, for a fieldworker to measure, mark and leave the nest area following these protocols.

In all years, subsequent monitoring visits were made every five or six days until completion, with additional visits two days before and one day after the predicted hatching date. Unless the nest had failed, field workers did not approach close to the nest on subsequent monitoring visits minimising sign, scent or tracks. On such visits, an observer would first try to observe the female leaving the nest area from a vehicle positioned at a distance >150 m. If the female was seen incubating or in the proximity of the nest, the nest was considered active and the observer retreated without closer approach. If the female was not seen, the observer would continue approaching on foot and observe the nest through binoculars from a distance of > 10 m to assess whether the nest was still active (incubating female seen, or eggs visible and fresh female tracks indicating female recently incubating) or had a final outcome (empty, chicks or egg shell in scrape). Closer visits were only made following nest completion (final outcome) thus minimising scent or track disturbance to the vicinity of any active nest. Installation and use of the nest cameras did not have any adverse effect on incubating females; none of 36 camera-monitored nests were deserted and videos ($n = 9$) showed that females resumed incubation an average of 28.2 minutes (SD ± 5.1) after camera installation and did not pay attention to the lens. Modelled daily nest survival (dsr) did not differ with presence of nest cameras (ΔAIC = -1.7 on removal, controlling for year), and was similar for nests with (97.7%; $n = 35$ nests; 429 exposure days) and without cameras (97.0%; $n = 61$ nests; 683 exposure days).

Section 2. Prediction of hatching date

For nests found during 2013-2015, incubation stage of the clutch at finding was estimated from egg measurements following Combreau *et al.* (2002), in order to then predict hatching date and plan subsequent visits. Egg weight at laying (‘fresh egg weight’, W_f) was estimated from egg dimensions following Hoyt (1979) as:

$$W_f = K_w \cdot LB^2$$

where L = length (mm), B = width (mm) and K_w = species-specific weight coefficient, taken as 0.00055 g.mm^{-3} for houbara, see Combreau *et al.* (2002). The incubation stage (day of incubation at nest finding, IS) was calculated from the average incubation period for houbara, 23 days (Combreau et al. 2002), as:

$$IS = 23 * (W_f - W)/(W_f - W_p)$$

where W = weight at finding (g) and W_p = pre-hatch weight (g), calculated from W_f assuming average weight loss of a houbara (both species) egg across incubation of 17.4% (Saint Jaime and van Heezik 1995). Hatch date was then predicted from the estimated incubation date (as date at finding + [23 – IS]). Laying date (date of clutch initiation) was calculated from estimated incubation date, accounting for clutch size and laying rate (eggs laid on alternate days, (Maloney 2003; Saint Jaime and van Heezik 1995)), assuming incubation starts when the penultimate egg is laid (RJB pers. obs., Maloney 2003).

For 71 nests for which hatching date was accurately known (from visits at hatching, females with behaviour monitored by satellite telemetry, or from nest cameras and temperature loggers, see section A3 below), observed date was strongly related to predicted hatch date ($R^2 = 0.95$; $p = 0.001$) (Fig. ESM3), with mean error of 2.4 days (n = 71 nests, SD ± 1.6 days), low relative to the span of the nesting season (e.g. 45-50 days in most years, see Fig.ESM1). Thus estimated lay dates provide a robust measure of potential seasonal effects.

Section 3. Assessing nest fate and camera monitoring of livestock disturbance

Failure was attributed to predation if predator footprints and/or other marks (tail, claws), broken eggshell and/or congealed yolk were found; and was attributed to trampling when hoof prints were found in and around the scrape, combined with egg remains and congealed yolk and/or eggs moved (i.e. kicked) out of the scrape. Video footage from 34 nests (8 nests in 2014, 24 nests in 2015) for which outcome was known, monitored for a total of 407 camera/days, validated interpretation of hatching and failure signs. Date and time of nest outcome were confirmed using nest cameras and temperature loggers for 60 nests in 2014 and 2015. As in other ground nesting species (Sheldon et al. 2013), scrapes of successful nests typically contained small to medium egg fragments (validated by nest cameras, Table ESM1), and their shape is flatter, as a consequence of chick movements around the rim (validated by nest cameras); chick tracks may also be visible around the nest depending on substrate and wind. Number of chicks hatched was inferred from clutch size, excluding any unhatched chicks, known partial predations or chicks dead in or near the scrape, and could sometime be confirmed by counting chick tracks close to the scrape. Thus hatchability will have been overestimated if some dead chicks or unhatched eggs were removed or scavenged; we attempted to minimise this possibility by visiting nests two days before and one day after hatching (see Section A1 above). For nests of females monitored by satellite telemetry the exact date of nest outcome (if not video-monitored or not known from visit at hatching) was inferred remotely through female behaviour: small and slow movement away from the nest (hatched at least one chick, with females with chicks leaving nests within 24 h from hatching) or large and fast movement away from nest without returning to the nest site (lost/abandoned nest); with a subsequent validation visit to the scrape.

Temperature loggers showed four out of 11 instances of unattributed nest predation occurred at night (12 pm – 06 am), consistent with predation by mammals (most likely foxes, though possibly feral dog *Canis familiaris*, or jackal *Canis aureus*) and excluding desert monitor *Varanus griseus* and people. The time of the other seven unattributed predation events was unknown. Although no incidence of fox predation of wild houbara nests was captured on video, a fox (*Vulpes vulpes/corsac)* was filmed predating one nest of a captive-bred female, confirming this mammal as one of the active nest predators. Hedgehog (from larger size on video tentatively identified as *Paraechinus hypomelas*, though *Hemiechinus auritus* cannot be ruled out) may be associated with clutch reduction in houbara nests, with evidence from nest cameras recording one failed attempt by a hedgehog to roll away an egg with the female defending it and two incidences of hedgehogs rolling away single, most likely abandoned eggs.

At nine nests monitored in 2014 by nest cameras for a total of 122 days, females were observed to interrupt incubation due to sheep disturbance at five of these nests, involving 11 events in 98 camera-days, with a mean rate of female displacement at these nests of 0.12 day^{-1} (SE ± 0.03 day^{-1}). However, in an additional 13 instances when sheep approached a nest, the female remained incubating. It was not possible to accurately estimate "flushing" distance due to camera focus length and limited field of view; hence, it was not possible to test whether distance to nearest sheep differed between instances when females were displaced and when they remained incubating. The majority of disturbance events detected (both with and without female displacement, n = 24) occurred within three hours after sunrise and three hours before sunset, with relatively mild ambient temperatures (mean 16.5 °C; SD = 6.8; range = 4–33.5). This pattern most likely relates to the daily movements of sheep flocks away and back to camps/wells, when flocks cover larger distances and are more likely to pass a nest. The three nests for which cameras recorded the highest number of sheep disturbance events (> 5) were located in medium to high sheep density areas (10–80 individuals km^{-2}).

Section 4. Sheep density estimates and GIS composite layer for livestock density

Transect-specific sheep densities were estimated separately for each year by conventional distance sampling (CDS) analysis, conducted in DISTANCE 6.0 (Thomas et al. 2010). Uniform, half-normal and hazard-rate detection models, with both cosine and polynomial adjustments (simple or hermite) were fitted, following Buckland et al. (2001). That with the lowest Akaike Information Criterion (AIC) was selected. Separate sets of models were examined across all detection functions after truncation of either 5% or 10% of the most distant observations, following Buckland et al. (2001); the truncation that provided the greater precision to the density estimate was selected.

Mean estimates of sheep density differed among years (Table ESM2), being similar in three years but greater in 2014. We consider this inter-annual variation to be due to both genuine differences in density among years and some variance among observers in different years. Inter-annual variance could be due to spring graminoid productivity; in years with good vegetation productivity flocks are larger as more lambs are left to graze instead of being slaughtered at a young age (< 1 week) in poor fodder years. However, differences in fieldwork team composition among years and type of transects (off-road in 2012, on road or track in 2013 and 2014) may also have contributed to inter-annual differences in methodology. Although laser range finders were used to measure perpendicular distance, for large or widely spread flocks there may be systematic bias among individual observers in estimating the 'flock centre'; furthermore differing attentiveness of observers may affect whether more distant flocks were observed (with a notably lower Effective Strip Width, ESW, in 2014 see Table ESM2). However, although density may be inflated in 2014, within each year the spatial pattern of relative sheep density is considered reliable. Year-specific interpolated density surfaces (with 500 m raster resolution) were created from transect-specific density values assigned to transect centroids, using the Inverse Distance Weighting (IDW) tool in ArcMap 10.1. The spatial pattern of these year-specific sheep densities (mean density extracted within 8 km x 8 km grid cells, n = 35) within the study area (minimum convex polygon based on nest extent) were strongly correlated among years (Table ESM3).

Comparison with Soviet-era georeferenced topographic maps (Military Topographic Directorate 1985-1991) showed 45.1% of current camps (n = 105) overlaid locations of camps in the 1970s, also suggesting considerable stability of camp and sheep distribution. Based on this evidence of stability of inter-year livestock distribution, we mapped a composite sheep density layer surface by distance-weighted averaging across the pooled transect centroids (n = 1,692) from all four years (Fig.ESM5).

Mean sheep density (*sheep density*) was then sampled within one-kilometre radius buffers around nest locations. One-kilometre radius buffers (area = 3.14 km^2) were considered appropriate relative to the area utilized by an incubating female (mean 50% kernels = 0.24 km^2; mean 85% kernels = 1.49 km^2; n = 13 home ranges; MK unpubl. data). Mean sheep density (pooling across years) was classified as: low = 0–10 individuals km^{-2}, medium = 11–30 km^{-2} and high = 31–80 km^{-2}, following Koshkin et al. (2014).

Supplementary tables

Table ESM1 Validation by nest cameras of initial interpretation of hatching and failure signs; overall classification accuracy (excluding unknown outcomes) = 93%.

	Video confirmation	
	hatched	**failed**
classified as hatched	**23**	**1**
classified as failed	**1**	**5**
classified as unknown		**4**

Table ESM2 Sheep density estimated from of year-specific distance analysis of transects driven in the Southern Kyzylkum, Uzbekistan. Mean density (inds/km^{-2}), survey effort and sample size, and Effective Strip Width (ESW) are also shown.

	2012	**2013**	**2014**	**2015**
Mean density (95% CIs)	16.7 (11.8-19.6)	23.4 (19.3-28.4)	65.5 (49.1-87.2)	24.2 (15.1-39.0)
Survey effort (km)	3,500	4,735	1,750	1,485
N flocks	294	331	149	164
ESW (95% CIs) (m)	464.2 (382.2-563.2)	256.6 (227.6-289.8)	95.5 (81.7-111.4)	286.5 (201.9-406.4)
Encounter rate (flocks per km)	0.08	0.06	0.08	0.10

Table ESM3 Correlations between year-specific sheep densities extracted as means from 8 km x 8 km grid cells (n = 35) within the area of nest extent across the four study years (minimum convex polygon, excluding two nests in *Artemisia* and nests outside the study area).

	2012	***2013***	***2014***	***2015***
2012	1			
2013	0.63	1		
2014	0.96	0.65	1	
2015	0.61	0.74	0.65	1

Supplementary figures

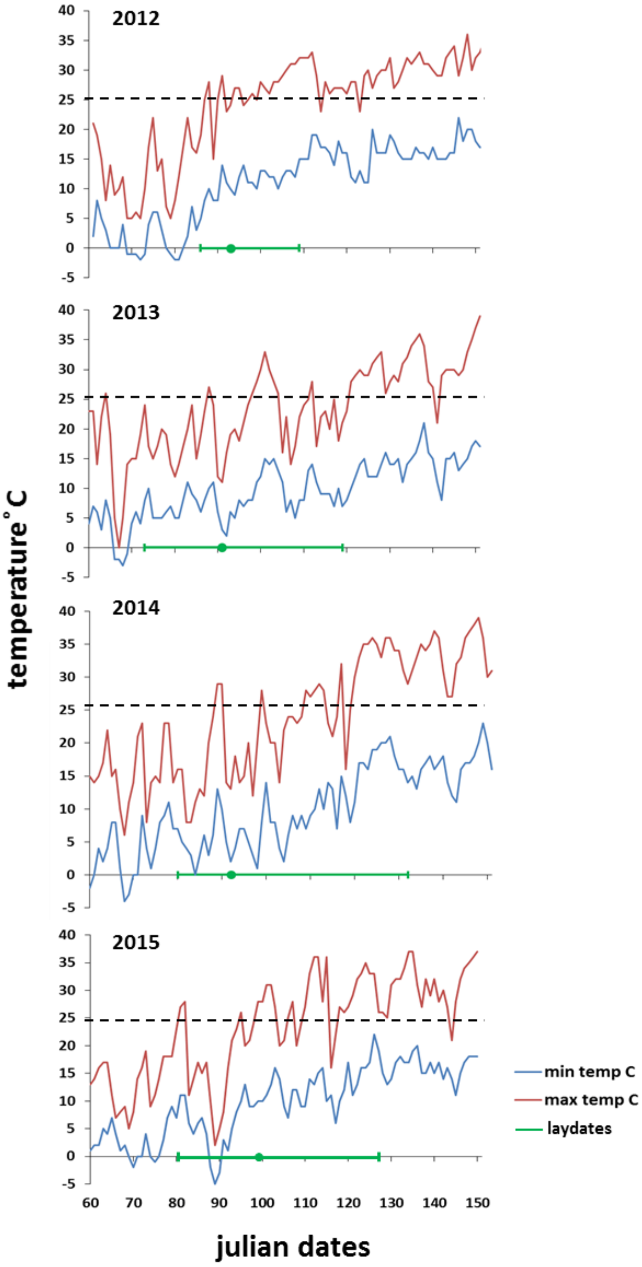

Figure ESM1 Laying periods of Asian houbara in each of four study years (green dot represents median laydate, green line represents full range of lay dates) in relation to spring maximum and minimum daily temperature in southern Kyzylkum, Uzbekistan. Dashed line shows the 25 °C threshold, Julian dates represent the period between 1-2 March (60) and 30-31 May (150). The span of the nesting season may have been under-estimated in 2012.

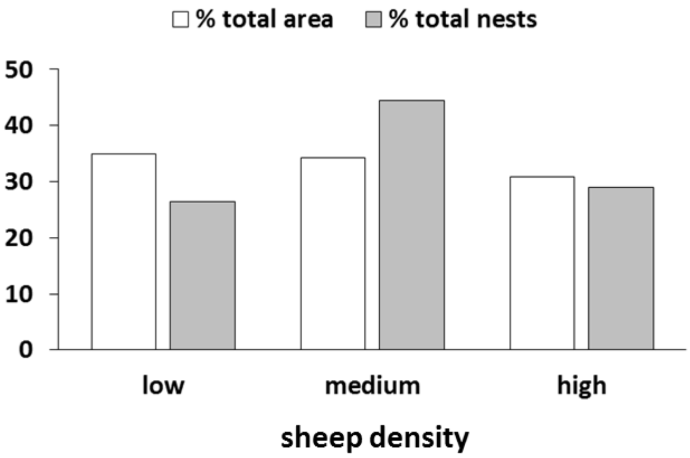

Figure ESM2 Proportion of the study area (14,300 km² of potentially suitable for Asian houbara habitat) under different sheep grazing pressures (low = 0–10, medium = 11–30 and high = 31–80 inds. km^{-2}, pooling across four years) and proportion of the total nests (n = 161) found within these areas.

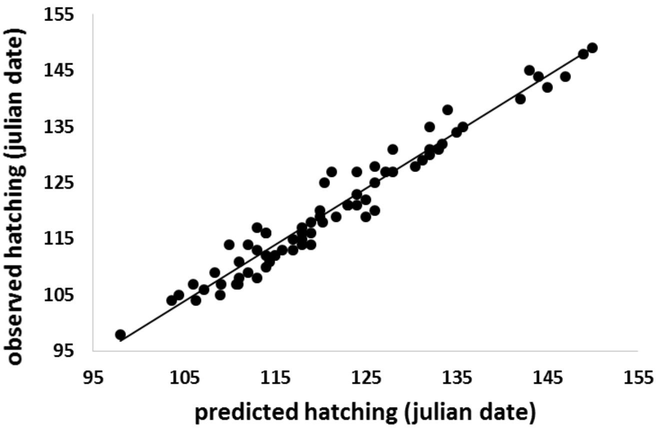

Figure ESM3 Relation between observed and predicted hatching dates for 71 wild houbara nests monitored during 2013–2015 , for which exact hatching date was known.

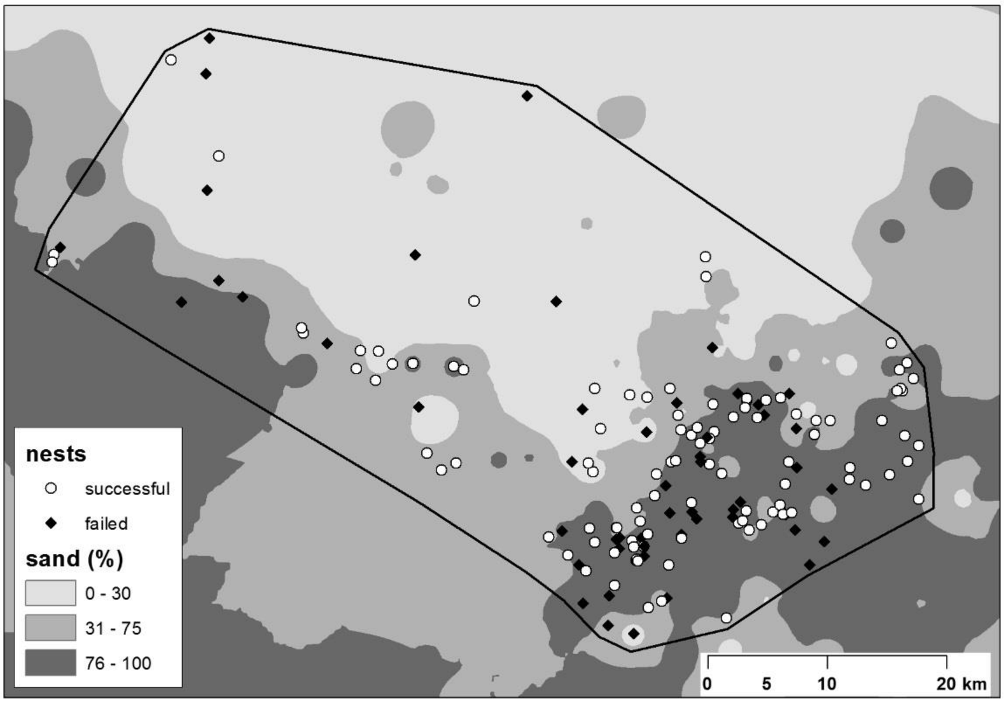

Figure ESM4 Percentage cover of consolidated sand (estimated over four replicate 2 m x 2 m quadrats around each nest, control and point count location; Koshkin et al. in press), with nests overlaid. Areas with low percentage cover of consolidated sand are dominated by clay.

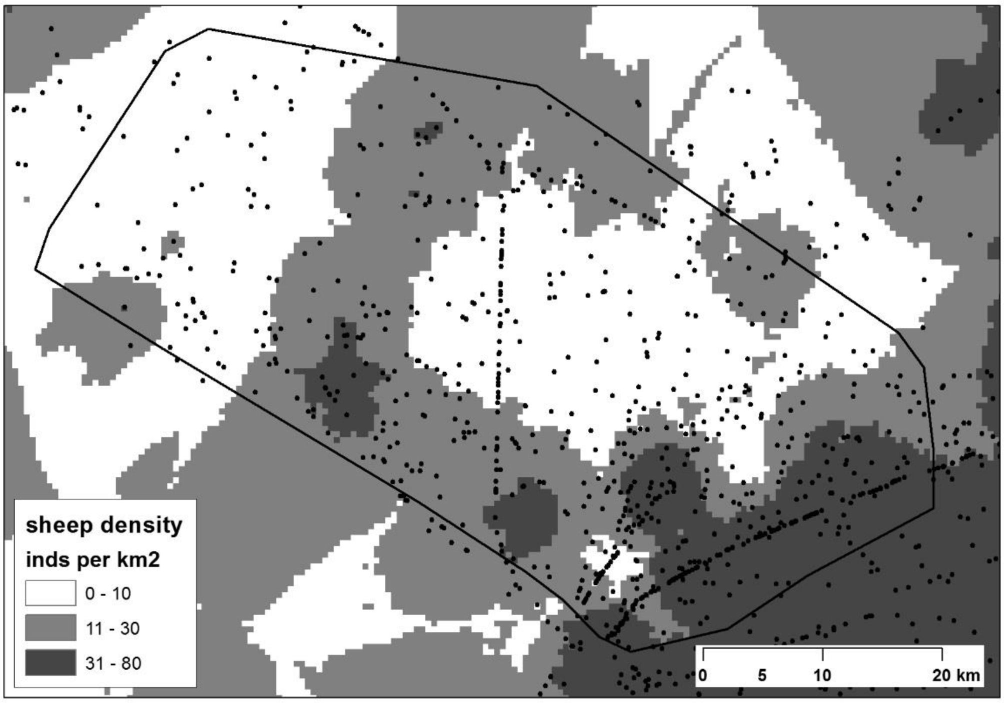

Figure ESM5 Distribution of transect midpoints in the study area for transects used to estimate sheep densitiy (inds/km^{-2}) during 2012-2015, subsequently used to create interpolated (inverse distance weighting) surface of sheep density.

Supplementary references

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. and Thomas, L. 2001. Introduction to distance sampling: estimating abundance of biological populations*,* Oxford, Oxford University Press.

Combreau, O., Qiao, J., Lawrence, M., Gao, X., Yao, J., Yang, W. and Launay, F. 2002. Breeding success in a Houbara Bustard *Chlamydotis* [*undulata*] *macqueenii* population on the eastern fringe of the Jungar Basin, People's Republic of China. - Ibis 144: E45-E56.

Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weight of birds'eggs. - Auk 96: 73-77.

Ibáñez-Álamo, J.D., Sanllorente, O. and Soler, M. 2012. The impact of researcher disturbance on nest predation rates: a meta-analysis. - Ibis 154: 5-14.

Ibáñez-Álamo, J. D. and Soler, M. 2010. Investigator activities reduce nest predation in blackbirds *Turdus merula*. - Journal of Avian Biology 41: 208-212.

Koshkin, M. A., Collar, N. J. and Dolman, P. M. 2014. Do sheep affect distribution and habitat of Asian Houbara *Chlamydotis macqueenii*? - Journal of Arid Environments 103: 53-62.

Koshkin, M.A., Burnside, R.J., Collar, N.J., Guilherme, J.L., Showler, D.A., Dolman, P.M. (in press) Effects of habitat and land-use on breeding-season density of male Asian Houbara *Chlamydotis macqueenii*. Journal of Ornithology

Mallord, J. W., Dolman, P. M., Brown, A. and Sutherland, W. J. 2007. Nest-site characteristics of Woodlarks *Lullula arborea* breeding on heathlands in southern England: are there consequences for nest survival and productivity? - Bird Study 54: 307-314.

Maloney, R. F. 2003. Survival, breeding and movements of reintroduced Asiatic Houbara (*Chlamydotis [undulata] macqueenii*) in Mahazat as-Sayd reserve, Saudi Arabia. University of New England.

Military Topographic Directorate. 1985-1991. Soviet General Staff Topographic Maps. Moscow.

Saint Jaime, M. and Van Heezik, Y. 1995. Propagation of the Houbara Bustard*,* London, Keegan Paul International.

Sheldon, R. D., Kamp, J., Koshkin, M. A., Urazaliev, R. S., Iskakov, T. K., Field, R. H., Salemgareev, A. R., Khrokov, V. V., Zhuly, V. A., Sklyarenko, S. L. and Donald, P. F. 2013. Breeding ecology of the globally threatened Sociable Lapwing *Vanellus gregarius* and the demographic drivers of recent declines. - Journal of Ornithology 154: 501-516.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A. and Burnham, K. P. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. - Journal of Applied Ecology 47: 5-14.

Thompson III, F. R., Dijak, W. D. and Burhams, D. E. 1999. Video identification of predators at songbird nests in old fields. - The Auk 116: 259-264.

Chapter 5

Breeding and post-breeding range use and movements of Asian houbara *Chlamydotis macqueenii* in Uzbekistan

Abstract

Despite studies on different aspects of biology and migration routes of Asian Houbara *Chlamydotis macqueenii*, little is known about space use and movements of Central Asian migratory populations during breeding and post-breeding dispersal, although these include important stages such as chick rearing and moult, when resource and habitat demands may alter. A total of 37 Asian houbara were fitted with satellite transmitters during 2012–2015 in the Bukhara region of Uzbekistan. Tracking data were used to assess range use and movements of adult houbara, focusing on home range (HR) size, site fidelity of both males and females, movements of females with broods and post-breeding space use of both sexes. Kernel smoothing was used to quantify home ranges for most of these behavioural/seasonal stages, with *href* bandwidth applied to unimodal HR's and *ad hoc* (*href**0.50) bandwidth to all birds with multimodal HRs. To examine and compare vegetation at breeding and post-breeding sites, growing season integrated NDVI was considered, calculated as the mean of NDVI values across seven 16-day composite periods of the growing season (March till June) for 2013. Houbara home range sizes varied with sex and season. Males were more faithful to display sites than females to nesting sites, displaying on average within 1.1 km (*SD* = 0.8, range = 0.1–2.2, n = 6) from the site used in the previous year. The majority of females exhibited relatively strong inter-annual fidelity to their general breeding area, however were even more site-faithful between successive attempts within a season. During post-breeding dispersal birds of both sexes utilised sites located on average over 130 km away from breeding sites, and these post-breeding locations were found to be more productive than breeding home ranges in terms of growing season NDVI values. The findings presented here provide knowledge on some of the least studied aspects of the Asian houbara ecology and hopefully will inform future conservation and management of this declining species.

Introduction

Recent advances in satellite telemetry technology, particularly the availability of smaller, lighter GPS transmitters, have greatly improved the efficiency of bird tracking, with increased frequency and quality of location fixes providing detailed temporal and spatial data for tracked individuals (Tomkiewicz et al. 2010). Satellite telemetry is now frequently used in studies of migratory birds (Villers et al. 2010, Terraube et al. 2012, Kessler et al. 2013, Klaassen et al. 2014, Willemoes et al. 2014) and allows the identification of the most crucial sites for different life stages (e.g. breeding, migration or wintering), as well as assessments of associated local habitat, land-use, threats and other factors, to inform potential conservation and management interventions.

Asian houbara *Chlamydotis macqueenii* (hereafter houbara) is a mostly migratory bustard species, ranging across deserts and semi-deserts from the Arabian Peninsula to Mongolia (BirdLife International 2015). A large proportion of the population breeds in Central Asia and winters mainly in Iran, Afghanistan and Pakistan, whereas several smaller breeding populations located in Iran, Pakistan and the Arabian Peninsula are resident (BirdLife International 2015). The species was recently classified as globally Vulnerable (IUCN 2015), following the virtual extirpation of breeding populations in the Middle East and substantial population declines across its Central Asian strongholds, largely caused by unregulated hunting and poaching (Combreau et al. 2001, Tourenq et al. 2005, Riou et al. 2011).

Understanding temporal and spatial patterns of breeding and post-breeding space use is important for houbara management, especially in view of the species' declines throughout its range. Captive breeding and reintroduction programs are currently used as the solution to mitigate off-take from hunting and to reinforce exploited populations of both Asian and African houbara *Chlamydotis undulata* (Islam et al. 2012a, Chargé et al. 2014), with several large houbara breeding centres functioning in different parts of the two species' range, annually releasing large numbers of captive-bred birds into the wild. Although *in-situ* management of local populations may ultimately contribute to the conservation of the houbara and would be preferable to *ex-situ* interventions, its potential is hindered by a lack of knowledge of several important stages of the species' annual life cycle. To optimise the chances of success with such management, a good knowledge is needed of the wild birds' biology and of different stages of their life history relating to the overall reproductive success and post-breeding space use of the species.

Despite studies on different aspects of houbara biology (Combreau et al. 2002, Hingrat et al. 2008, Aghainajafi-Zadeh et al. 2010, Bourass and Hingrat 2015), and migration pattern (Combreau et al. 1999, Judas et al. 2006, Combreau et al. 2011), little is known about space use and movements of migratory populations during breeding and post-breeding dispersal. In terms of space use, most studies have focused either on African houbara (Hingrat et al. 2004, Hingrat et al. 2008) or small resident populations of Asian houbara inhabiting the Arabian Peninsula (Combreau et al. 2000, Islam et al. 2012b). Only two published studies have examined space use of Asian houbara populations in Central Asia (Judas et al. 2006, Riou and Combreau 2014). However, as the former focused on the breeding system and the latter mainly examined migration, their findings on space use and fidelity were reported only as additional, incidental information, with both studies focusing on males.

To divide annual location data into meaningful periods, studies involving populations of both houbara species (Combreau et al. 2000, Hingrat et al. 2008, Islam et al. 2012b) defined stages within a given year based on calendar seasons or seasonal weather pattern (e.g. summer, winter, rainy season). However, such broad and somewhat subjective definitions of different stages of the houbara's annual cycle may obscure a particular phase in the annual cycle in which potentially significant changes in spatial use take place. Both Hingrat et al. (2004) and Islam et al. (2012b), in studies involving resident wild breeding birds, reported that females had on average larger home ranges than males. A resident population of reintroduced captive-bred birds in Saudi Arabia possessed mean home ranges that were similar in size for males and females, but were larger in the rainy season than in summer or winter (Combreau et al. 2000). None of these three studies treated the chick-rearing period as a separate stage of the female's annual cycle, although space use by a female with a brood is expected to be different from that in the nesting period, as shown, for example, for Little Bustard *Tetrax tetrax* (Lapiedra et al. 2011). Lack of published information relating to this stage is not surprising, however, considering how secretive females with broods are and that not only the female but also, ideally, the chicks need to be tracked. Even then, considering the mortality rate among chicks, it remains very difficult to obtain a reasonable sample of females with broods tracked for weeks. Combreau and Al Baidhani (*in litt.*) described movements of females with broods, gave examples of distances moved by a brood per day and showed that ranges of neighbouring broods may overlap. With this exception, there is otherwise no information available on range use by females and broods, a circumstance which limits conservationists' capacity for the effective management of breeding populations.

Some species may require different habitats and resources after breeding, and disperse from the nesting area in order to find other food sources, to escape the summer heat and/or to moult (Todd et al. 2007, Barta et al. 2008, Mitchell et al. 2010, Sara et al. 2014). Similar requirements are also found in bustards (Silva et al. 2007, Alonso et al. 2009, de la Morena et al. 2015). For houbara, no studies of post-breeding spatial patterns have been conducted; the only evidence in this regard is that after ceasing their display activity two males moved to a different location, subsequently remaining there over three and four months respectively, before starting their southward migration (Judas et al. 2006). Such behaviour could well be linked to moult, as birds in mixed stocks of captive houbara (both species) started to moult during (males) or immediately after breeding (females) (Saint Jalme and van Heezik 1995). Captive Asian houbara held within a breeding flock at a specialist breeding centre in southern Kyzylkum, and with access to *ad libitum* food, moulted from the beginning of June untill the end of August (K. Scotland personal communication), coinciding with the end of the breeding season of the wild birds and first half of the post-breeding period. Body mass in the middle of the moulting period was found to be at its lowest while food intake was at its highest, even higher than that at the beginning of the breeding season (Saint Jalme and van Heezik 1995). This suggests that post-breeding birds might be constrained to move to new areas with higher resources (following possible depletion of resources around leks and nesting sites) in order to moult and recover after the energy-demanding breeding season. To identify such sites is clearly of relevance to conservation and management, as the post-breeding period might constitute a substantial part of the species' annual life cycle and conditions at these sites may directly affect not only the birds' migratory success but their survival through the annual cycle.

Many bird species that breed in habitats with relatively stable ecological conditions (habitat structure, availability of resources and shelter) such as, for example, old-growth forests or permanent wetlands, exhibit a high degree of fidelity to their nesting sites and breeding territories (Hoover 2003, Meszaros et al. 2006, Jahn et al. 2009, Schlossberg 2009, Viter 2013). In a heterogeneous desert environment, with inter-annual and seasonal variations in habitat quality, resource availability, precipitation and temperatures, the animal inhabitants can be expected to exhibit high levels of ecological flexibility. Although such breeding site characteristics as habitat structure are unlikely to change greatly between seasons and years, spatial and temporal availability of resources may vary greatly. Throughout the year Asian houbara rely on a mixed diet of mainly invertebrates and plants (Tigar and Osborne 2000, Gubin 2004), and although invertebrates seem to dominate their diet, the prevalence of different groups (e.g. ants, beetles) may vary depending on season (Gubin 2004), with similar variation reported for African houbara (Bourass et al. 2012, Bourass and Hingrat 2015). Furthermore, unpredictability of desert conditions between years (dry or wet) and seasons (late/early spring, dry/wet summer) may strongly affect the abundance as well as the spatial and temporal distribution of houbara food. Additionally, Paradis et al. (1998) showed that migrant birds disperse further from the previous breeding site than resident birds. Taking all these factors into consideration, it is reasonable to expect that the home range sizes and site fidelity of houbara to vary with year, season and/or sex in response to variations in local food availability.

To date, knowledge of Asian houbara breeding site fidelity is limited. Riou and Combreau (2014) reported high inter-annual and intra-seasonal fidelity of males to display sites for a population in Kazakhstan, while Judas et al. (2006) found that one male was faithful to its breeding site in China. However, one would expect females to be less faithful in their choice of nesting sites than males in their choice of display territories, as the former are likely to re-nest in new areas, responding to factors such as changing resource distribution or nesting success in the previous year (if affected by predator distribution). For example, Hoover (2003) showed that breeding site fidelity of male Prothonotary warblers (*Protonotaria citrea*) increased with breeding success of the previous season. Additionally, travel and time costs of dispersal between successive nesting attempts (intra-seasonal site fidelity) maybe greater than during return migration, as incubation and repeated egg production are likely to consume large amounts of energy. Understanding the degree of site fidelity in houbara and how this is influenced by previous breeding experience is important, as this could help to improve the effectiveness of the protection and management directed to a particular area of a desert.

This study is the first to assess range use, movements and site fidelity of Asian houbara in its Central Asian strongholds, focusing on breeding and post-breeding periods and taking into account discrete stages of houbara range use. The following hypotheses are tested: (1) home range sizes vary with sex and stage, (2) inter-annual fidelity to breeding areas is affected by previous breeding experience and (3) is less pronounced than distance between successive nesting attempts within the same season, (4) females with chicks utilise larger home ranges than females when incubating owing to their greater mobility, (5) between the termination of breeding and the onset of migration both males and females use similar areas, that are different from their breeding sites due to differing habitat and resource requirements during that stage.

Methods

Study area

All wild birds were captured and fitted with satellite transmitters in the Bukhara region of Uzbekistan, within an area of around 1,000 km^2 located approximately 70 km northwest of the city of Bukhara in the southern Kyzylkum Desert. The landscape is predominantly flat, with distinctly different shrub-desert communities determined by variations in topography, geomorphology, drainage and soil, but all dominated by drought-resistant and/or halophytic shrubs (Koshkin et al. 2014). Subsequently, all locations of the tagged birds within particular seasons were used for analysis, including locations from sites used by tagged birds beyond the study area (including other regions of Uzbekistan, southern Kazakhstan and northern Turkmenistan).

Satellite transmitter deployment

For catching houbara, lines of leg snares were used, set around display sites and nests. To minimise the risk of stress and injury, snares set for catching females were checked within one hour. To catch males, snares were set just after sunset (when display activities had terminated) and were checked early in the morning, giving a male approximately an hour long window to be caught after the start of display activity at sunrise. Videos of captures showed that neither males nor females struggled when caught and instead crouched and remained still until catchers arrived. As handled bustards are prone to myopathy (Spraker et al. 1987, Höfle et al. 2004), catches were conducted with caution and the catching team undertook repeated training, following strict protocols, to reduce handling time (less than 20 minutes, including blood sampling). Of the total 37 catches, 32 passed without incident or injury, with the exception of one mortality (caused by stress to the trapped female from a monitor lizard that approached the snared bird) and four minor incidents caused by snares: two shallow cuts to upper tibia area when snares closed higher on the leg, one injured toe and a bleed near the toe (all these injuries were treated prior to the birds' release). There were no incidents of myopathy and with the exception of the one female, all birds survived at least several months after release. Catching of females was assumed to be sufficiently traumatic to potentially cause nest desertion, so all females were caught early in the season to maximise their chances of re-nesting, and their eggs were removed for artificial incubation at a specialist houbara breeding centre. Satellite transmitters (PTT-100 Argos/GPS solar-powered; Microwave Telemetry Inc.; initially involving a few 45 g PTTs, subsequently only 30 g PTTs) were fitted using "backpack" harnesses made of Teflon tubular tape (0.25 mm). The 3–5% body weight threshold (Murray and Fuller 2000, Barron et al. 2010) was followed, so that birds were fitted with transmitters only if they weighed more than 900 grams (for 45 g PTT 5%, 30 g PTT 3.3 % of bodyweight). All birds were released where they were caught, immediately after being fitted with satellite transmitters.

Satellite telemetry data

Satellite transmitter duty cycles differed among individuals and were adapted through the study in an attempt to conserve batteries and maintain long-term use of the transmitters. For instance, the ground-track option on female transmitters (for locating females with broods using antennas) was set to be activated only for a particular part of the season (when juveniles were old enough to be tagged) and remained active only for 2–4 hours per day during this period. Additionally, during the hot midsummer period, after birds were found to be using shrubs for shade throughout most of the day (J. Burnside personal observations) thus decreasing solar panel exposure to the sun, the number of fixes was reduced to avoid battery drain on latter duty cycles. As another measure to prolong battery life, no fixes were taken during the night (with the exception of two units), as daytime activity was originally considered to be more important for the study aims. Most transmitters were set to record six fixes per day during the breeding season and a reduced number in the post-breeding period, transmitting data every three days. All locations used were GPS fixes (± 18 m accuracy), with the exception of one set of locations from an ARGOS unit, of which only the best-quality (class 3, <250 m accuracy) fixes were used. For some units there were periods of unstable transmission due to low battery, presumably caused in some instances by feathers covering the solar panel and preventing the battery from charging. Quality of transmissions often decreased during the period of summer heat when batteries did not receive enough charge, resulting in transmission failure and gaps in data. In addition, the majority of transmitted fixes for nesting females were often from the same location, owing to the high proportion of time females spent on the nest incubating.

Sampling and season definitions

Preliminary exploration of satellite-tracking data suggested that houbara space use outside the wintering and migration periods could be divided into several distinct life-history stages. When examining home ranges, for females these stages were defined as: nesting (laying and incubation), chick-rearing (2 stages) and post-breeding; and for males as: display and post-breeding. Multiple nesting attempts of a female within a given breeding season were treated as separate 'stages' during analysis, and models included female ID as a random effect to control for repeated observations from the same individual. Movements spanning periods between nesting attempts, as well as between the failure of the last nesting attempt and the onset of the post-breeding stage, were assumed to be of less significance, usually spanning short periods of time and thus were not considered in the analysis.

The female nesting stage was considered to start with the first egg and end on the day of nest outcome. The laying date of the first egg was back-calculated from the start of incubation, identified from the behaviour of satellite-tagged birds, assuming eggs are laid on alternate days (Saint Jalme and van Heezik 1995, Maloney 2003) and incubation starts when the penultimate egg is laid (Robert Burnside personal observations, Maloney 2003). Exact date of nest outcome was inferred remotely through female behaviour: slow, short-distance movements away from the nest without returning to it (indicating at least one chick hatched), or rapid, relatively long-distance movements away from nest, again without returning to it (indicating a failed nest). These inferences were validated as far as possible by a subsequent visit to the scrape (see Chapter 3 for details).

The female chick-rearing period was considered to start from the day following hatching and to last either until the female separated from the brood, with chick independence at approximately 52 days (R. Burnside unpublished data), or until the female lost the brood. These two possible outcomes were inferred from (a) an inspection of both female and tagged chick locations until the day they separated and (b) an evaluation of the speed and distance of the female's movements; distances over 30 km, twice the maximum daily distance of 15 km covered by a brood as recorded in this study, clearly indicated brood loss. Smaller chicks were expected on average to cover shorter distances, so the size of the home range of a female with a brood will largely depend on the period at which the brood was monitored. Therefore, chick-rearing period was split into two stages, (1) with chicks <14 days old and (2) with chicks >14 days old. Females which did not have chicks, lost their chicks early or did not initiate a subsequent nesting attempt usually entered their post-breeding period earlier (see definition below).

During the breeding season adult males hold territories at which they display (Hingrat et al. 2008, Riou and Combreau 2014). In characterising male display home range size and location, all fixes were used for the period starting from the male's arrival at the display site, inferred from a change to short-distance local daily movements (approx. 3 km per day) centred around a central location (lek), following a rapid long-distance (usually >30 km per day) migratory movement northwards into the study area. The display stage was considered to end the day before a long-distance movement (usually >30 km per day) away from (and without return to) the display area. Two males caught in 2015 were not restricted in their movements to a particular area following catching on 28 and 30 April 2015, and instead utilised relatively large territories, without staying anywhere for long (movements of one of these males shown in Fig.1). As the resulting large home ranges were not related to 'classic' display activity, these two samples were not considered when comparing home range sizes. It is possible that capture stress terminated display activity of these males, or that they were sub-adults prospecting at a dominant male display site when captured.

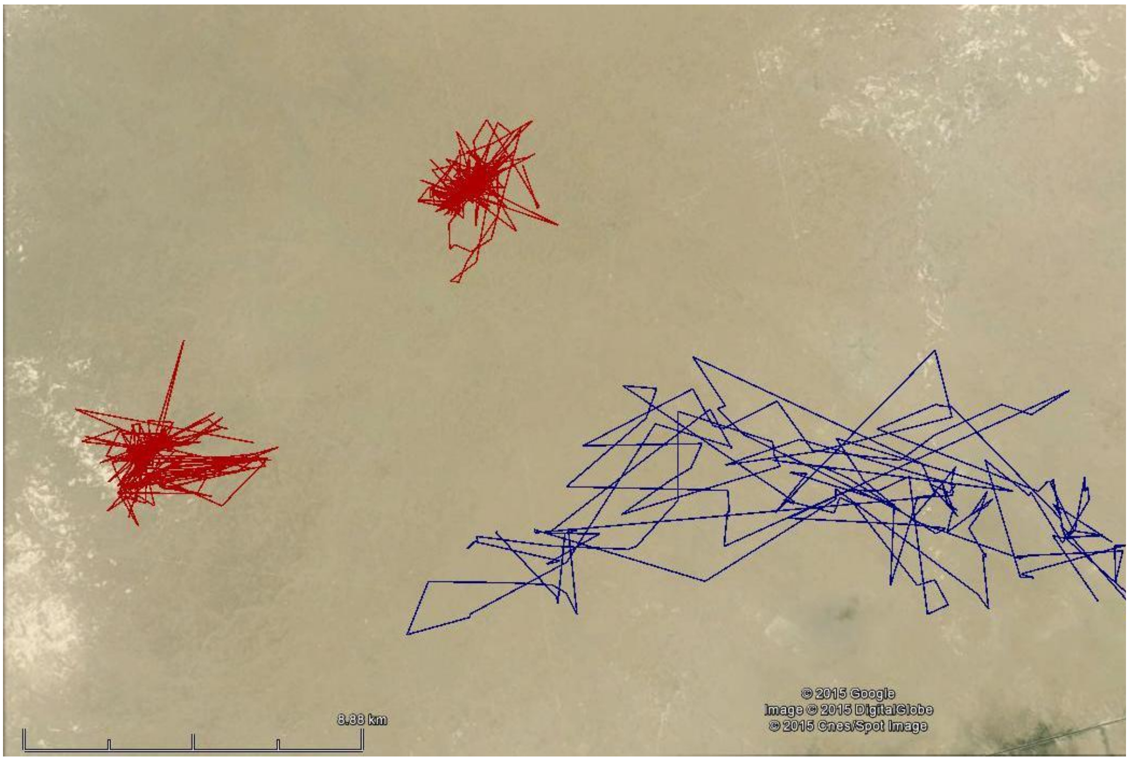

Figure 1. Examples of 'classic' display behaviour (movements of two males, April – June, red) and behaviour of a male without a fixed territory (May–June, blue), prior to movement to post-breeding sites.

The start of the post-breeding period for both males and females was inferred from the first fixes after they became relatively stationary (mean daily movements <3 km), following a long-distance movement from the previously used breeding site. Often using small (<100 km^2) sites, birds would normally spend the time remaining until the southward migration (2–4 months), presumably moulting (R. Burnside personal observations of, e.g., feathers in roost sites of PTT birds).

Home range estimation

One of the earliest attempts to define an area used by an animal is the definition of home range (HR) by Burt (1943) as the: 'area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range.' The most important issue raised by this definition is that there is a need to define the core area used by an animal in order to be able to exclude occasional locations related to some exploratory or incidental movements. This definition also implies that home range extent of a particular animal may vary in size within a given period of time, depending on the animal's stage in the annual cycle. Minimum convex polygons (MCP), used earlier to define home ranges, have more recently been replaced by analysis of 'utilisation distribution', a relative frequency distribution of locations (Fieberg and Kochanny 2005, Keating and Cherry 2009), most frequently quantified by a kernel-smoothing density estimation technique (Fieberg 2007, Laver and Kelly 2008).

To quantify the utilisation distribution of houbara, the kernel-smoothing technique was used. Kernels can be fixed (smoothing parameter is the same for all locations within the home range of an individual) or adaptive (smoothing is adjusted depending on the density of locations) (Worton 1989). Fixed kernels may often over-smooth or under-smooth data that has heterogeneous spatial distribution (Worton 1989); adaptive kernels were therefore used as more suitable for the data, which contained a higher density of points within core areas and fewer outlying points within the MCP outer perimeter. Selection of the appropriate bandwidth (parameter controlling the degree of smoothing/complexity) is, however, considered far more important than the choice between fixed or adaptive kernels (Seaman and Powell 1996). Reference bandwidth (*href*) is one of the most commonly used smoothing methods; although appropriate for unimodal data (Silverman 1986), this may over-smooth multimodal data (home ranges with >1 core area, separated by unused, or sparsely used, areas) (Fig.2a). Another commonly used approach is to reduce reference bandwidth to a fixed proportion (*href*proportion*), applied to multiple individuals to reduce over-smoothing (Bertrand et al. 1996, Kie et al. 2002). This method performs better with multimodal kernels, as was in case with the analysed data (Fig.2b). The proportion value is selected by eye, depending on the nature of the data. The least-squares cross-validation (LSCV) smoothing method was not applied as it tends to be especially sensitive to sample size, and with large numbers of locations it often results in under-smoothing (resulting in small HR perimeters around individual data points: Fig.2c) (Kie et al. 2010). Therefore, after thorough inspection of the data and comparison of outputs of different methods, I used *href* bandwidth for birds with unimodal HRs and a single *ad hoc* (*href**0.50) bandwidth for all birds with multimodal HRs.

Only home ranges based on >50 locations, as a recommended minimum to draw adequate kernels (Seaman et al. 1999), were used in the analysis of home ranges.

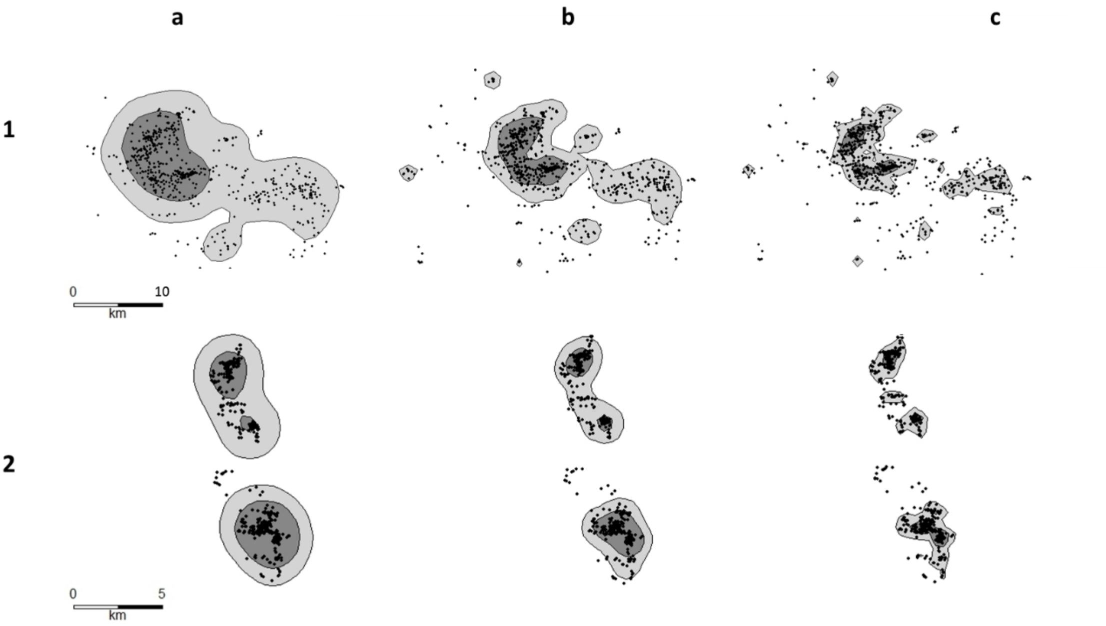

Figure 2. Examples of unimodal (1) and multimodal (2) Asian houbara post-breeding home ranges in the southern Kyzylkum, Uzbekistan; showing 85% (light grey) and 50% (dark grey) kernels resulting from using *href* (a), *href*0.50* (b) and *LSCV* (c) smoothing methods.

Habitat data

Normalized difference vegetation index (NDVI) is based on a calculated ratio of red to near-infrared wavelengths reflected by the earth's surface and measured by satellites (Goward et al. 1991). This measure of photosynthetic biomass has been demonstrated to correlate positively with field measurements of primary productivity of vegetation and vegetation biomass in a number of environments (Pettorelli et al. 2005). Although there has been limited use of remotely sensed vegetation indices (VIs) in semi-arid or arid areas, such areas produce fewer issues with saturation and fewer problems with clouds than areas with denser vegetation (e.g. forest canopies) often experience (Chappell et al. 2001). However, there are some issues associated with the use of remote-sensed VIs in semi-arid regions (Franklin et al. 1993), as the reflected measures can be 'noisy' owing to high temporal and spatial variability of vegetation and the dominance of bare ground, with differing reflectance and spectral properties among soil types due to roughness, organic matter, colour, moisture and/or salt content (Franklin et al. 1993, Weiss et al. 2004, Gessner et al. 2013).

To examine and compare vegetation at breeding and post-breeding sites, I used the MODIS product (Carroll et al. 2013), which aggregates data from each of 22 16-day periods across the year, into a single NDVI value for each 1 km raster cell. We considered growing season integrated (GSi) NDVI, covering seven 16-day periods between 6 March and 26 June and calculated as the mean of NDVI values across the growing season for each pixel. This metric is widely used to describe the annual productivity of vegetation (Pettorelli et al. 2005) and is likely to perform better in arid/semi-arid areas than NDVI integrated across the full year, as it does not include less vegetated winter values affected by soil reflectance noise. For the southern Kyzylkum, GSi NDVI was considered to be a good proxy of vegetation cover, as it was found to correlate strongly with total winter precipitation (October to May), the main driver of primary vegetation productivity; and to correlate weakly but significantly with field measures of density of perennial shrubs (C. Panter, unpublished analysis). Similar results were reported for Central Asian deserts, where observed correlations between one month composite NDVI and winter monthly precipitation were strongest with a 4-6 month lag (Gessner et al. 2013).

Preliminary data exploration showed that GSi NDVI varied among years, but was consistently greater in *Artemisia* habitat, lower in *Calligonum*, and slightly lower again in the three remaining habitats (*Astragalus*, *Salsola arbuscala* and *S. rigida*) that each had similar mean NDVI values to each other (Fig.3). As the annual variation in mean habitat-specific GSi NDVI was marked, these were subsequently related to winter rainfall (8 months, October-May inclusive; source: Global Precipitation Climatology Project). Winter rainfall explained more than half of the variation in the annual mean GSi NDVI for each shrub community ($n = 9$ years), with strongest relationship with *Artemisia* habitat ($R^2 = 0.582$) and weaker relationship with the other four communities: *Calligonum* ($R^2 = 0.426$), *Astragalus* ($R^2 = 0.494$), *Salsola arbuscula* ($R^2 = 0.429$) and *Salsola rigida* ($R^2 = 0.463$).

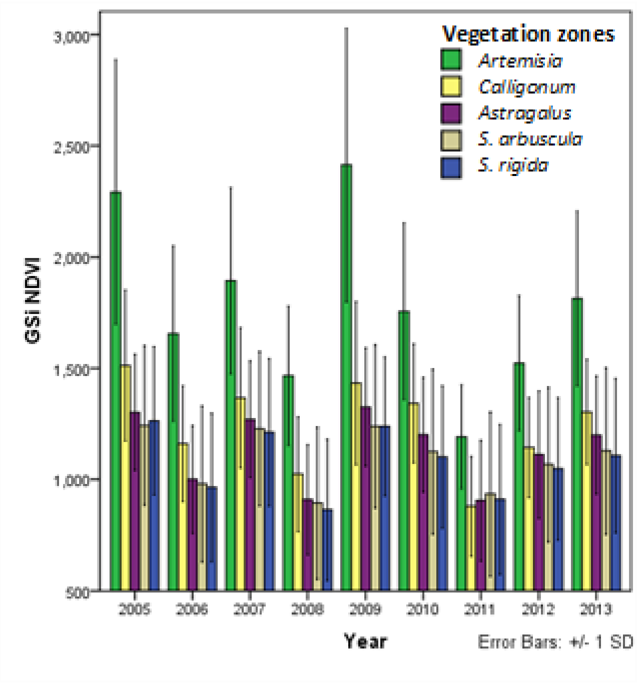

Figure 3. Annual mean (± *SD*) GSi NDVI within each of five shrub assemblages (see Chapter 4 for classification) for 9 years (2005-2013). Source: C. Panter, (unpublished analysis)

For the southern Kyzylkum, the relative spatial pattern of NDVI was found to be very stable across years (2005–2013) (C. Panter, unpublished analysis), despite inter-annual variation in overall mean index related to rainfall. GSi NDVI pixel-specific values (n = 20,705 pixels) were strongly correlated for each pair of years compared across 9 years (mean Person's $R^2 = 0.886$). The strongest correlation was found for two wetter-than-average years (2005 and 2009; $R^2 = 0.952$), with lowest correlation observed between 2005, the wettest year, and 2011, the driest year of the examined nine year period ($R^2 = 0.683$) (C. Panter, unpublished data). Therefore it was considered appropriate to use NDVI data from 2013 only, representing an average year in terms of precipitation and overall mean NDVI values, as a stable representation of vegetation structure across years. No additional treatment was applied to raw 16-day composite NDVI rasters, as individual day-specific errors and missing individual day values (due to clouds) were eliminated through averaging across 16 days, whereas extreme or negative composite-specific values were found only for completely un-vegetated areas (extensive saltpans and waterbodies), which were masked and excluded from the analysis, or occurred in winter due to reflectance from snow (C. Panter, unpublished data), with neither considered in this study.

Most post-breeding sites used by birds monitored by this study fall outside of the area of vegetation sampling. Therefore, to be able to compare vegetation between breeding and post-breeding in terms of broad shrub assemblages, breeding and post-breeding home range centroids were overlaid on vegetation map produced by Rachkovskaya (1995), reclassified into broad communities by grouping sub-communities with similar dominant perennial shrubs.

Statistical analysis

When comparing home range sizes among different stages and between sexes, 50% kernels were generated for both males and females, except for the female nesting stage. For the latter, 85% MCPs were used, as kernels that include multiple repeated fixes from the same point (nest) are unstable whereas excluding duplicate fixes from the nest scrape location resulted in insufficient number of locations to draw reliable kernels. MCPs were reduced to 85% to exclude outlying locations, considered to represent infrequent exploratory movements.

HR kernels were drawn and their areas were measured using the 'adehabitatHR' package. As home range sizes were not normally distributed, they were log-transformed prior to analysis. Effects of season and sex on home range area sizes were modelled in generalised linear mixed models (GLMM) with Gamma error, including bird ID (to control for multiple kernels between years, and for nests, within years also) as a random effect.

Inter-annual site fidelity of females returning to breed during at least one consecutive year after the year they were caught was examined by comparing distances between the first nesting attempts in each year. Additionally, for each returning female, distances between the last nesting attempt in one year and the first nesting attempt in the subsequent year were compared. Post-breeding site fidelity was examined by comparing distances between post-breeding home range centroids of two consecutive years. For the year that a female was first caught, the nest where caught was considered as first nesting attempt, as all nests were initiated within the range of the laying dates of the first nesting attempts of returning satellite-tagged females (range = 20 March–17 April, n = 13). Intra-seasonal site fidelity of females was examined by comparing the distance between consecutive nesting attempts within the same breeding season (including nests at which the female was initially caught). For males, the degree of site fidelity was examined by measuring the distance between display location centroids (50% kernels) from two or more consecutive seasons. Kernel overlap was not used for testing site fidelity owing to the extremely small home ranges of many individuals, particularly females, which do not overlap even when close to each other. Distances between nesting attempts and between stages were measured using the 'sp' package in R 3.1.1 (R Core Team 2013) and were square-root transformed to normalise the data prior to analysis; bearings were calculated using the 'circular' package in R. The effect of failure reason (catching or natural cause) on distance and duration of movement between consecutive nesting attempts was modelled in GLMMs with Gamma error, controlling for year as fixed and female ID as random effects.

Total daily distance travelled by broods was measured using the 'adehabitatLT' package in R, with probable underestimation of daily distances considering that the distance between the last location of the previous day and the first location of the given day was not included in calculations. However, as females with broods are assumed not to cover long distances during the night, their first morning location (6–7:00 am) was unlikely to be very far from the last location on the previous evening (21–22:00 pm). Effects of maximum daily temperature on total daily distance moved by broods were explored in GLMM with Gamma error, including female ID as random effect and age (days) as fixed affect. Daily maximum temperature data for the Bukhara meteorological station was downloaded from: (http://www.wunderground.com).

All GLMM models were run in R using the 'MuMIn' package.

Results

A total of 37 wild houbara were satellite-tagged during 2012–2015 (Table 1A,B). Of these the majority were females (n = 25), providing 31 nesting, 18 chick-rearing and 38 post-breeding stages, after 17 stages were excluded from home range analysis (owing to insufficient numbers, or poor quality of fixes) and including an overall average of 277.8 locations per female stage (*SD* = 244.2) (Table 1A). Over 80% of the total 46 nests of satellite-tagged females were subsequently visited and locations confirmed using hand-held GPS units. Satellite telemetry of 12 males provided 15 display and 14 post-breeding stages, after the exclusion of four stages with insufficient sample sizes (Table 1B).

Twenty females (80%) re-nested at least once within the same breeding season after being caught, with the subsequent re-nesting attempt on average 9.2 days (*SD* = 2.1) after catching. After initial capture, majority of males (75 %) quickly returned to the area where they had been caught, on average 1.2 days (*SD* = 0.4) after catching, and resumed holding their territory.

Table 1. Time ranges and number of fixes for breeding and post-breeding seasons of female (A) and male (B) Asian houbara *Chlamydotis macqueenii* in Bukhara district, Uzbekistan. (----) indicate absence of data for a given season (birds did not display, nest or have chicks); (NU) indicates given seasons were not used in the analysis of home ranges due to low sample size (< 50) or unsuitable quality of fixes.

A		**nesting**			**chick rearing**			**post-breeding**		
name	**PTT ID**	**from**	**till**	**fixes**	**from**	**till**	**fixes**	**from**	**till**	**fixes**
Aiol	114120c	24/04/2013	02/05/2013	NU	------------	------------	------	02/06/2013	28/10/2013	624
Aiol	114120c	11/04/2014	18/04/2014	NU	------------	------------	------	------------	------------	------
Aiol	114120c	27/04/2014	22/05/2014	118	23/05/2014	18/07/2014	266	22/07/2014	19/09/2014	264
Aiol	114120c	29/03/2015	24/04/2015	121	25/04/2015	28/06/2015	313	30/06/2015	25/08/2015	261
April	127695a	------------	------------	------	------------	------------	------	24/06/2013	04/11/2013	840
April	127695a	09/04/2014	22/04/2014	99	------------	------------	------	10/06/2014	28/10/2014	870
Bistra	145072	------------	------------	------	------------	------------	------	06/06/2015	24/08/2015	251
Blueeggs	49812a	24/04/2012	18/05/2012	184	19/05/2012	28/07/2012	418	30/07/2012	28/09/2012	514
Blueeggs	49812a	20/03/2013	26/03/2013	71	------------	------------	------	------------	------------	------
Blueeggs	49812a	07/04/2013	28/04/2013	213	lost chicks early		------	23/05/2013	01/11/2013	1253
Blueeggs	114128	30/03/2014	18/04/2014	205	------------	------------	------	08/09/2014	25/10/2014	200
Carex	145061	26/04/2014	29/04/2015	NU	------------	------------	------	------------	------------	------
Carex	145061	08/05/2015	14/05/2015	NU	------------	------------	------	10/08/2015	26/08/2015	NU
Chepon	145051	24/04/2015	26/04/2015	NU	------------	------------	------	------------	------------	------
Chepon	145051	04/05/2015	28/05/2015	116	29/05/2015	22/06/2015	117	05/07/2015	26/08/2015	141
Chiroyli	145069	02/05/2015	12/05/2015	52	------------	------------	------	30/07/2015	25/08/2015	79
Clangula	127700	11/04/2015	07/05/2015	172	lost chicks early		------	21/05/2015	23/08/2015	618
Daenarys	127689a	24/04/2013	19/05/2013	NU	------------	------------	------	04/07/2013	11/10/2013	459
Daenarys	127689a	16/04/2014	06/05/2014	67	------------	------------	------	07/05/2014	08/10/2014	986
Daenarys	127689a	04/04/2015	28/04/2015	NU	------------	------------	------	------------	------------	------
Daenarys	127689a	10/05/2015	31/05/2015	NU	01/06/2015	15/07/2015	NU	31/07/2015	23/08/2015	361
Ferula	127698a	15/04/2013	13/05/2013	232	14/05/2013	20/07/2013	476	22/07/2013	27/10/2013	612
Kamalak	145060	22/04/2015	15/05/2015	108	16/05/2015	16/06/2015	151	30/07/2015	26/08/2015	78
Khaleesi	127694a	------------	------------	------	------------	------------	------	25/07/2013	10/11/2013	491
Khaleesi	127694a	06/04/2014	30/04/2014	137	lost chicks early		------	stopped transmitting		------
Khiva	127692a	20/04/2013	15/05/2013	130	16/05/2013	28/05/2013	104	01/06/2013	11/11/2013	950
Khiva	127692a	25/03/2014	21/04/2014	135	22/04/2014	22/06/2014	446	26/06/2014	07/10/2014	662
Khiva	127692a	02/04/2015	24/04/2015	145	25/04/2015	30/05/2015	235	08/07/2015	25/08/2015	246
Koyan	129479b	------------	------------	------	------------	------------	------	11/07/2014	12/10/2014	491
Lucky	145071	30/04/2015	17/05/2015	82	------------	------------	------	20/05/2015	22/08/2015	347
May	127703	13/04/2015	20/04/2015	NU	------------	------------	------	05/07/2015	23/08/2015	298
Pioda	114126b	29/04/2014	23/05/2014	138	24/05/2014	14/07/2014	266	16/07/2014	25/08/2014	184
Pioda	114126b	30/03/2015	03/04/2015	NU	------------	------------	------	------------	------------	------
Pioda	114126b	14/04/2015	07/05/2015	NU	08/05/2015	22/07/2015	108	23/07/2015	26/08/2015	79
Quyosh	145065	05/05/2015	29/05/2015	110	30/05/2015	07/07/2015	171	20/07/2015	25/08/2015	108
Salsola	127690a	11/04/2013	08/05/2013	179	09/05/2013	15/06/2013	280	16/06/2013	07/08/2013	416
Salsola	127690a	01/04/2014	17/04/2014	54	------------	------------	------	10/07/2014	10/10/2014	583
Salsola	127690a	03/04/2015	24/04/2015	127	------------	------------	------	------------	------------	------
Salsola	127690a	29/04/2015	15/05/2015	101	------------	------------	------	06/06/2015	23/08/2015	401
Shamol	145049	21/04/2015	26/04/2015	NU	------------	------------	------	------------	------------	------
Shamol	145049	06/05/2015	08/05/2015	NU	------------	------------	------	------------	------------	------
Shamol	145049	17/05/2015	08/06/2015	110	09/06/2015	26/07/2015	182	30/07/2015	26/08/2015	81
Su	145066	03/05/2015	25/05/2015	115	26/05/2015	12/06/2015	79	26/06/2015	24/08/2015	167
Un	145055	02/05/2015	24/05/2015	97	25/05/2015	20/07/2015	211	22/07/2015	24/08/2015	90
Utur	145043	27/04/2015	18/05/2015	98	19/05/2015	28/07/2015	273	30/07/2015	24/08/2015	81
Yaushan	127701a	------------	------------	------	------------	------------	------	23/06/2013	06/10/2013	707
Yaushan	127701a	11/04/2014	06/05/2014	149	------------	------------	------	------------	------------	------
Yaushan	127701a	11/05/2014	20/05/2014	54	------------	------------	------	06/07/2014	30/09/2014	526
Yaushan	127701a	13/04/2015	05/05/2015	124	06/05/2015	13/07/2015	482	17/07/2015	25/08/2015	240
Yomgir	145044	17/04/2015	22/04/2015	NU	------------	------------	------	------------	------------	------
Yomgir	145044	10/05/2015	21/05/2015	NU	------------	------------	------	03/08/2015	25/08/2015	51
total birds				**20**			**14**			**24**
total seasons				**31**			**18**			**38**

B			**display**			**post-breeding**	
nick	**PTT ID**	**from**	**till**	**# fixes**	**from**	**till**	**# fixes**
Blue	114200d	08/04/2014	16/05/2014	NU	09/06/2014	27/10/2014	58
Adam	127685a	02/04/2013	03/06/2013	422	stopped		------
Bobo	49785b	07/05/2014	26/05/2014	222	27/05/2014	27/10/2014	514
Bobo	49785b	03/03/2015	11/07/2015	1101	stopped		------
Nasreddin	49645a	09/05/2013	14/06/2013	312	28/06/2013	26/08/2013	607
Aral	127707a	03/04/2013	14/06/2013	500	15/06/2013	12/11/2013	799
Aral	127707a	05/03/2014	16/05/2014	423	-------------	-------------	------
Muzhik	127688a	11/04/2013	24/06/2013	495	30/06/2013	07/11/2013	761
Muzhik	127688a	03/03/2014	07/06/2014	587	10/06/2014	08/11/2014	865
Muzhik	127688a	10/03/2015	02/07/2015	634	06/07/2015	23/08/2015	235
wild2011	49810a	27/03/2013	10/06/2013	904	29/06/2013	01/10/2013	1103
wild2011	49810a	19/03/2014	23/05/2014	726	01/06/2014	18/09/2014	1031
wild2011	49810a	25/03/2015	12/06/2015	932	15/06/2015	26/08/2015	548
Bukhara	129480b	01/05/2015	06/06/2015	137	07/06/2015	05/07/2015	100
Gerboa	127707b	01/05/2015	02/07/2015	234	23/07/2015	25/08/2015	NU
Rambo	127699c	28/04/2015	02/07/2015	NU	27/07/2015	25/08/2015	88
Oxus	129485c	30/04/2015	08/06/2015	NU	10/06/2015	25/08/2015	166
Saxaul	129482c	29/04/2015	08/06/2015	158	15/06/2015	25/08/2015	133
total birds				**9**			**10**
total seasons				**15**			**14**

Breeding and post-breeding phenology

After first arrival on the breeding grounds (defined as a 50 km radius buffer around the subsequent nest location), females started incubation and became 'stationary' on average 12 days (*SD* = 4.2 days, range 1–21 days) later. The start of the female nesting period varied among the four years (range 14–24 March), with the latest known nest hatching on 8 June in 2015.

Mean date of chick hatching for the broods of satellite-tagged females (considering all nesting attempts) was 15 May (*SD* = 13.2 days, range = 21 April–8 June). First chick-rearing period (young chicks) ranged from 22 April till 23 June, second chick-rearing period (older chicks) ranged from 24 May till 28 July.

Males arrived at their display sites (and were assumed to start display immediately upon arrival) on average on 10 March (n = 6 stages of 4 returning males; range 3–25 March) and left these sites on average on 11 June (n = 14 stages of 11 males; 16 May–11 July). Most of the males arrived directly in the area of the display site, with an average delay of 1.2 days (range 1–3 days) between arrival on the breeding grounds (defined as 50 km radius buffer around the subsequent display home range centroid) and becoming 'stationary' around the display site.

On average, males started moving to the post-breeding areas on 20 June (*SD* = 16.2 days, n = 15 stages, range = 1 June–27 July), females on 5 July (*SD* = 24.3 days, n = 39 stages, range = 7 May–8 September).

Home range size

Female nesting areas were on average approximately 80 times smaller than areas used by females with broods under two weeks old and more than 500 times smaller than areas used by females with chicks over two weeks old (Table 2). Home range size was similar between female nesting areas and male display areas (removal of term for *sex*, ΔAIC = -1.5). Female and male post-breeding areas were also similar in size (removal of *sex* ΔAIC = -2.0) (Table 2). The majority of individuals of both sexes had relatively small, compact post-breeding home ranges, but several birds (both sexes) utilised much larger areas.

Table 2. Mean, standard deviation (SD) and range (min, max) of area sizes (km^2), for male and female Asian houbara at different stages of the breeding season, showing number of home ranges (HR) and of individuals (ind) contributing to the sample of home ranges and mean number of tracking-days per HR stage class (days) for each sex and stage.

period	Home range area (km^2)				Sample size (N)		
	mean area	*SD*	min	max	HR	ind	days
Female							
nesting (85% MCP)	6.1	6.6	0.4	27.1	30	20	17.3
chick rearing 1 (50% kernel)	513.7	1,129.1	27.8	5,096.5	19	14	14
chick rearing 2 (50% kernel)	3,435.8	4,219.7	62.1	14,176.0	17	13	35
post-breeding (50% kernel)	3,215.2	8,945.1	5.6	52,507.6	38	24	68.7
Male							
display (50% kernel)	38.7	55.0	0.5	180.4	15	9	65.2
post-breeding (50% kernel)	2,617.7	4,486.0	39.9	16,618.0	14	10	89.5

Inter-annual site fidelity

Of seven females that returned in at least one subsequent year after the year in which they were caught; six returned to breed in two and one female in only one subsequent seasons, providing a total of 13 first-nesting attempts monitored in years after the original catching year. Only four of these 13 first-nesting attempts were successful, with other females re-nesting at least once after failure of the first attempt. Five of these females returned each year to the same general area when selecting nest sites, nesting on average 12.1 km (*SD* = 15.1, range = 0.8–50.6 , n = 9 stages) from their first nesting attempt of the previous breeding season (Fig.4). For the same five females, distance between the last nesting attempt of the previous year and the first nesting attempt of the following year (mean = 13.3 km, *SD* = 21.8, range = 0.6–70.1, n = 9 stages) did not differ from the distance between first nesting attempts of two consecutive seasons (mean 12.1 km, *SD* 15.1) in a GLMM with Gamma error, controlling for female ID as random effect (ΔAIC = +0.4 on removal of *distance*). The other two females were less site-faithful, in 2014 nesting 190.7 km and 225.8 km respectively from the first nesting location in the 2013 season. However, in 2015 both returned to nest closer to the first nest location of the 2013 season (0.7 and 93.4 km respectively). Females showed low levels of site-fidelity to their post-breeding locations, returning to areas located on average 177.9 km (*SD* = 267.7, range = 0.9–763.2 km, n = 8 stages, n = 5 females) from the previous season 50% post-breeding kernel centroid. Of these, one of the two least site faithful females was also the least site faithful to her breeding site (see above) and the second female moved to a very different area following a second catching (to replace a satellite transmitter).

Males were faithful to their breeding season territory, returning to a display site on average only 1.1 km (*SD* = 0.8, range = 0.1–2.2, n = 6 stages) from the previous season 50% kernel display centroid (Fig.4). As with females, males also did not show a pronounced site fidelity to post-breeding sites, with an average distance of 48.9 km (*SD* = 98.3, range = 0.7–224.7, n = 5 stages, n = 3 males) between 50% post-breeding kernel centroids of two consecutive years. However, again the mean value was strongly influenced by one much less site-faithful male.

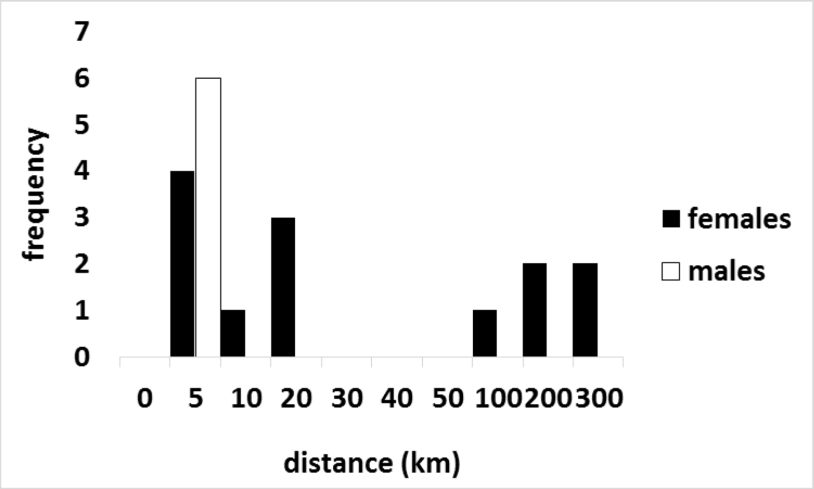

Figure 4. Distance between first nesting attempts of two consecutive seasons for 7 females (n = 13 stages) and between display location centroid of two consecutive seasons for 4 males (n = 6 stages).

Intra-seasonal site fidelity

Successive nesting attempts were located a mean of 24.8 km (*SD* = 52.4, range = 0.8 – 259.4) from the previous attempt within the same season. Females appeared to re-nest further away after catching (mean 32.6 km, *SD* = 63.9, range = 0.8–259.4; n = 17) than after losing a clutch to natural causes (mainly predation) (mean 12.7 km, *SD* = 24.3, range = 0.8–82.3; n = 11) (Fig.5), but the effect of cause of failure (anthropogenic or natural) was not supported in GLMMs with Gamma error, controlling for female ID as random and year as fixed effects (ΔAIC = +0.3 on removal of *failure reason*). Number of days between successive nesting attempts differed if the re-nesting birds were caught during the previous attempt (mean = 9.2 days, *SD* = 2.1) or lost their previous clutches to a natural cause (mean = 7.2 days, *SD* = 1.3; GLMM controlling for female ID as random and year as fixed effects, ΔAIC = +7.0 on removal of *failure reason*).

Distances between nesting attempts (all females) were greater for first-nesting attempts in consecutive years (mean = 53.8 km, *SD* = 91.0, range = 0.8–277.9, n = 19) than for intra-seasonal distances between consecutive nesting attempts (mean = 30.2 km, *SD* =58.1, range = 0.8–259.4, n = 22; GLMM with bird ID as random effect; ΔAIC = +7.6 on removal of *type of movement*).

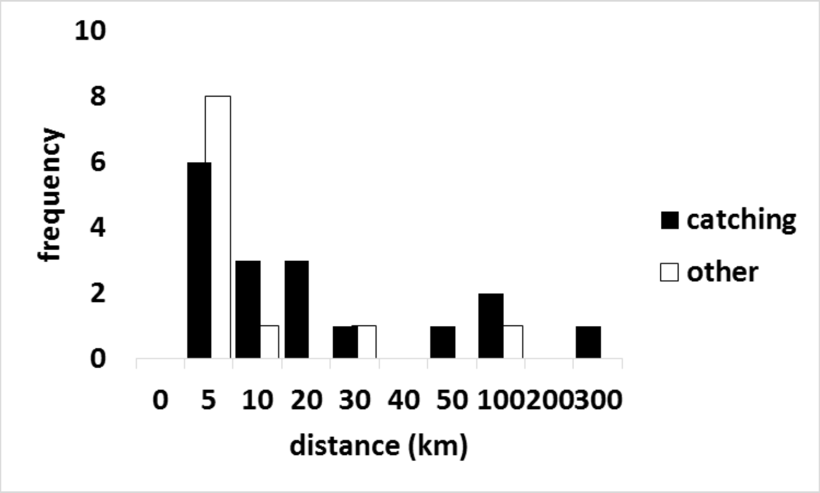

Figure 5. Distances between successive nesting attempts within the same season (n = 28 movements), for movements following female catching (n = 17) and other causes of nest failures (predation = 7, trampling = 1, failure with unknown cause = 3).

Chick-rearing period movements

Unsurprisingly, females with older chicks moved longer distances per day than those with younger broods (Fig.6). Maximum daily temperature was only moderately correlated with chick age (days) (n = 18 broods, Pearsons $r = 0.41$, $R^2 = 0.17$), allowing the inclusion of both age and temperature in models. Whether total daily distance moved by broods was related to maximum daily temperature, was examined in GLMMs that controlled for brood age as a fixed effect and female ID as random effect. The full model containing both maximum daily temperature and chick age, showing a significant negative effect of temperature on total daily distance moved, was more strongly supported than models incorporating only chick age or only maximum daily temperature (Table 3). This shows that, controlling for chick age, broods move shorter distances per day when temperatures are hotter.

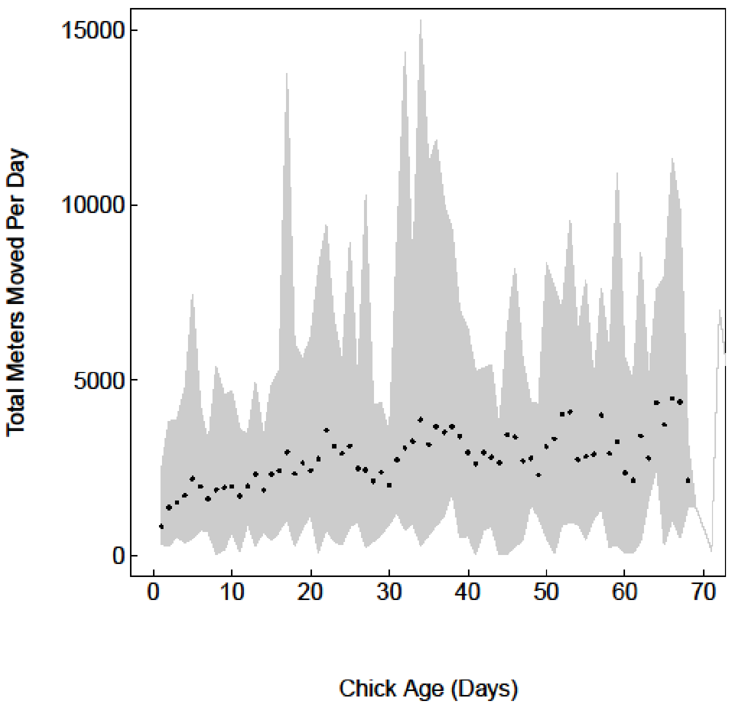

Figure 6. Change in total distance travelled per day (m) by females with broods (n = 18 broods, dots = mean, grey polygons = min and max) with chick age since hatching.

Table 3. Outputs of the generalised linear mixed models (GLMM) examining the effect of maximum daily temperature on cumulative daily distance moved by broods, controlling for female ID.

Model	AIC	*ΔAIC*	*B ± SE*
age	2667.7	0	-0.003 ± 0.0005
maxT			0.004 ± 0.002
age	2679.8	12.1	-0.003 ± 0.0004
maxT	2725.0	57.3	-0.003 ± 0.002

Post-breeding movements

Location centroids for female post-breeding home ranges were on average 130.1 km (*SD* = 119.9, n = 37 movements) from their nesting sites, with many females dispersing in a south-eastern direction after breeding (Fig.7a). As one of the few exceptions, on termination of its last nesting attempt one bird spent almost two months only 3.9 km away from its nest site before starting migration, whereas another individual travelled 523.3 km north to a post-breeding site in southern Kazakhstan. Location centroids for the male post-breeding stage were on average 177.8 km (*SD* = 140.9, n = 11 movements) from their display sites (Fig.7b). Post-migratory dispersal distances did not differ between males and females, with no support for the effect of sex on variable removal, controlling for bird ID as random effect (ΔAIC = -1.0). Similarly, angular direction of dispersal did not differ between the sexes (Watson-Williams Test, $F_{2,48}$ = 0.04, p = 0.834).

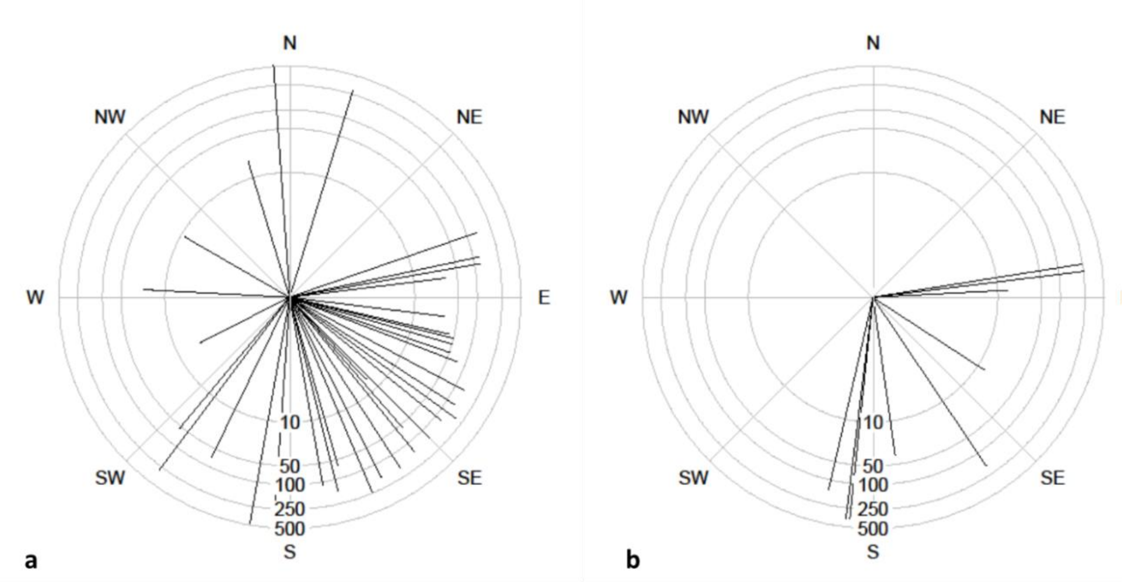

Figure 7. Distances (km, log-scale) and direction of movement from first nest attempt locations to post-breeding area location centroids for 37 female (**a**) stages and from display location centroids to post-breeding area location centroids for 11 male (**b**) stages.

Post-breeding sites on average had substantially higher GSi NDVI values than breeding sites (GLMM, controlling for birds ID as random and for sex as fixed effects; ΔAIC = 47.5 on removal of *stage* term) (Fig.8); and the effect was similar between sexes (ΔAIC = -1.9 on removal of *sex* term from model including *stage*).

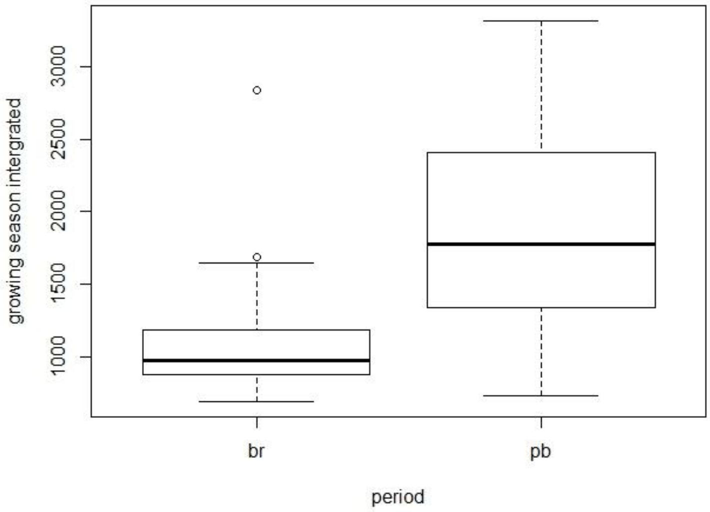

Figure 8. Growing season integrated NDVI at sites occupied during breeding (br) and post-breeding (pb) periods for both males and females, showing the median (horizontal line), quartiles (box) and range (bars) of the data.

Females with chicks reached their post-breeding site on average 9.1 days (SD = 12.4 days, n = 18 stages, n = 14 females) after separating from their brood or after losing it, with the majority stopping en route. A similar mean number of days (9.3 days, SD = 8.8, n = 14 stages, n = 10 males) was required for males to reach post-breeding areas after leaving their display territories (Fig.9). Females that were not successful in a particular breeding season, however, spent on average 52.1 days (SD = 38.7, n = 15 stages) elsewhere before reaching their post-breeding sites. Of those cases when females after termination of breeding spent more than a month before reaching post-breeding sites (n = 9 stages), in six cases the latter, surprisingly, were located to the north or northeast of the last nest location.

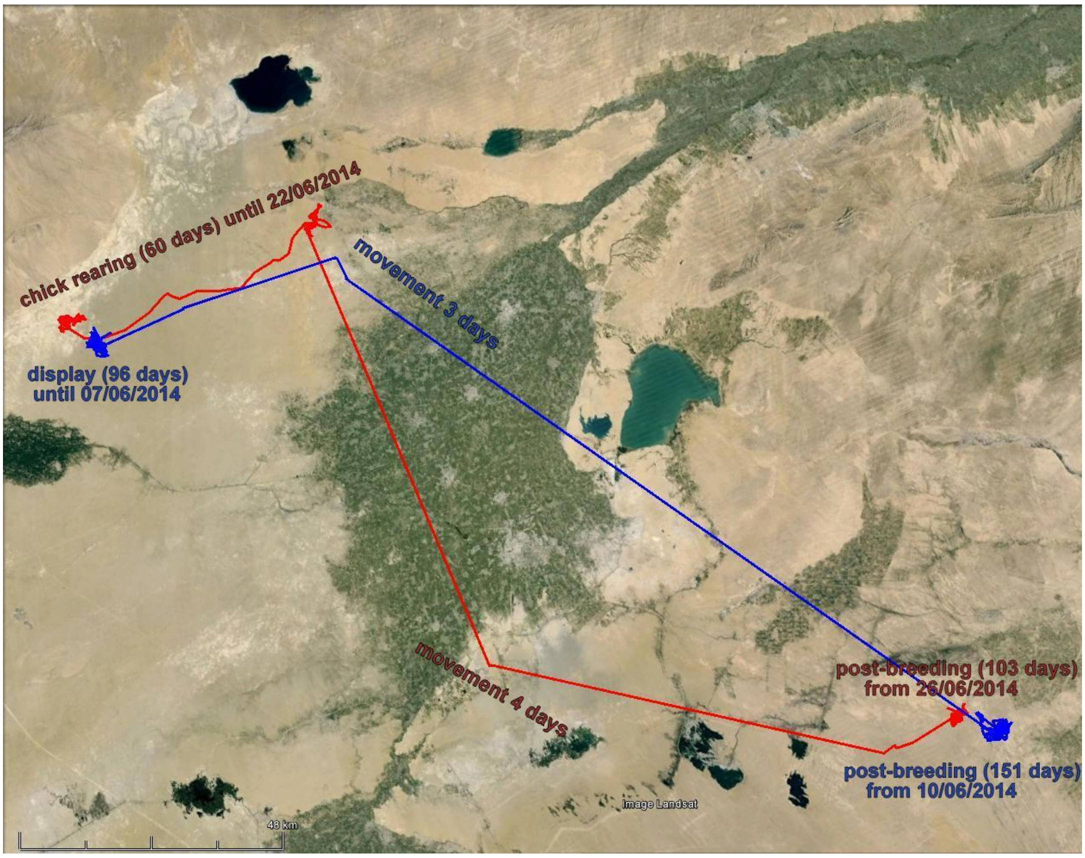

Figure 9. Typical post-breeding dispersal, showing the movement of a female (red) from an area used during chick-rearing, and the movement of a male (blue) from its display site, to respective post-breeding sites. Note: such a close proximity of male breeding and consecutive post-breeding sites to female sites is not typical.

Overlaying breeding (nesting and display) and post-breeding home range centroids on the seimi-arid shrub vegetation communities as mapped by Rachkovskaya (1995) showed that the majority of houbara were using *Astragalus* and *Salsola* dominated habitats during breeding, but were predominantly found in *Artemisia* dominated habitats during post-breeding dispersal (Fig.10)

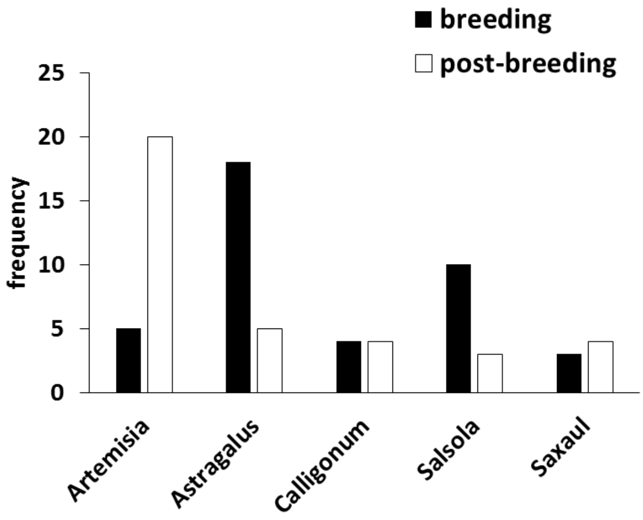

Figure 10. Frequency of locations of breeding (n = 40 stages) and post-breeding (n = 36 stages) home range centroids for both males and females in each of the five shrub assemblages, classified following Rachkovskaya (1995) and subsequently re-classified into broader assemblages based on dominant shrub species.

Discussion

Houbara home range sizes varied with sex and season. Although males were on average more faithful to display sites than females to nesting sites, surprisingly the majority of females also exhibited relatively strong inter-annual site-fidelity, albeit being more site-faithful within season. Following breeding, birds of both sexes moved to post-breeding sites, located on average over 130 km away from breeding sites, and used them for several months before undertaking migration. Post-breeding sites were more productive or contained greater density of vegetation in terms of growing season NDVI values.

Breeding space use and movements

Strong fidelity of males to display sites was also found by Riou and Combreau (2014) and by Judas et al. (2006) in migratory populations of Asian houbara. However, although the majority of females tagged in the present study returned to the same general area over multiple years, they may perhaps have moved further if a clutch was lost and showed some tendency to re-nest further away after being caught and handled. A similar response was observed in Tengmalm's Owls *Aegolius funereus*, which showed increased nest-hole shift and breeding dispersal distances following experimental predation risk by captive-bred minks, compared to control birds (Hakkarainen et al. 2001).

Hingrat et al. (2004) reported larger breeding home ranges for resident female African houbara (14 km^2 ± 12 [*SD*]; 50% kernels), compared to nesting home range reported in our study (6.1 km^2 ± 6.6 [*SD*]; 85% MCP). This discrepancy between studies is perhaps most likely related to the definition of 'breeding season' in Hingrat et al. (2004), which might have included chick-rearing period (not specified), or else it may reflect either different space use by the two species of houbara, different tracking techniques used (satellite- vs radio-tracking) and/or different methods used to quantify home ranges. On the other hand, 50% kernels of male display sites in our study (mean 38.7 km^2, *SD* = 55.0 km^2; range 0.5−180.4) were substantially larger than 75% kernels reported for breeding male Asian houbara in Kazakhstan, ranging from 0.4 to 1.1 km^2 (Riou and Combreau 2014) and 50% kernels of breeding male African houbara in Morocco (mean 1 km^2, *SD* = 1 km^2; range 0.1−4 km^2). With respect to the Moroccan data such a discrepancy is most likely related to different space use by the two species, as the reported mean distance between nearest male territories was almost twice as large in Asian Houbara (1.44 km, *SE* = 0.05; Riou and Combreau 2014) than in African houbara (0.86 km, *SD* = 1.01; Hingrat et al. 2004). However this is difficult to explain the discrepancy of our results with the findings by Riou and Combreau (2014).

Site fidelity

Strong inter-annual fidelity of males to their display sites might mean that prime display locations are crucial for male mating success, as such sites can possibly vary in terms of visibility, female densities or abundance of resources. Young males are likely more mobile during breeding season and probably often represent floaters – non-territorial males trying to steal matings by displaying next to mature males or otherwise intercepting females in the vicinity. However it is possible that during this period, by exploring the future breeding area, they finally select a suitable display location and hold on to it during the subsequent years. A quick return of males to the same display site they were caught at a day or two before again suggests that holding on to a particular display location is very important for males, even if they have to do this after surviving a traumatic experience of catching and handling.

Intra-seasonal fidelity of females to breeding areas was found to be stronger than inter-annual fidelity, which probably indicates high flexibility of the species and its ability to adapt to often unpredictable desert environments. If the location of a nest is determined by the conditions in the desert at the start of the breeding season then it seems hardly surprising that second breeding attempts in the same season should be relatively close by. Although structurally desert habitat (consisting mainly of perennial shrubs) is less likely to change substantially on a yearly basis, the local abundances of different houbara prey species (beetles, ants, arachnids, lizards, etc.) and annual plants are likely to vary between years, in response to winter precipitation or spring temperatures and possibly to some other local factors. Therefore, even after her first nest fails a female is likely to re-nest in the vicinity of the first site, as the new site is more likely to have similar conditions. If this is the case, then future work based on a larger sample of individuals and seasons, may be able to examine whether differences between years in patterns of breeding settlement after return migration show similar trends among females – as expected if females are settling in response to inter-annual variation in habitat quality.

Post-breeding space use and movements

The majority of birds utilised small post-breeding sites for a number of months, often remaining there longer than at breeding sites and sometimes returning to the same area in subsequent seasons. This suggests that post-breeding sites are likely to be rich in particular resources that can support a large bird within a relatively small area for long period of time. The extremely high temperatures these birds experience at this stage of the annual cycle, and their decreased activity when moulting, may help explain the small sizes of most post-breeding home ranges. However, most birds still remain in the same areas through September and October, when temperatures are lower and moulting is almost over. Another possible explanation of the small home range size of post-breeding birds is related to the daily duty cycles of the satellite transmitters used in this study. Although a study of captive-bred released Asian houbara in Saudi Arabia describes two main peaks of summer daily activity (at dawn and before sunset), the birds' activity, which the authors associate mainly with feeding, was also reported to increase on moonlit nights (Combreau and Launay 1996). Similarly, birds in the Kyzylkum could potentially be utilising larger areas to feed at night while remaining less active during the day due to the heat. As night fixes were not recorded for a majority of transmitters this information might have been missed. However, evidence from two birds equipped with transmitters set to take night fixes shows that, while they utilised different areas during the night (12 pm – 4 am) compared to daytime, they mainly remained within their daytime range extent (Fig.11).

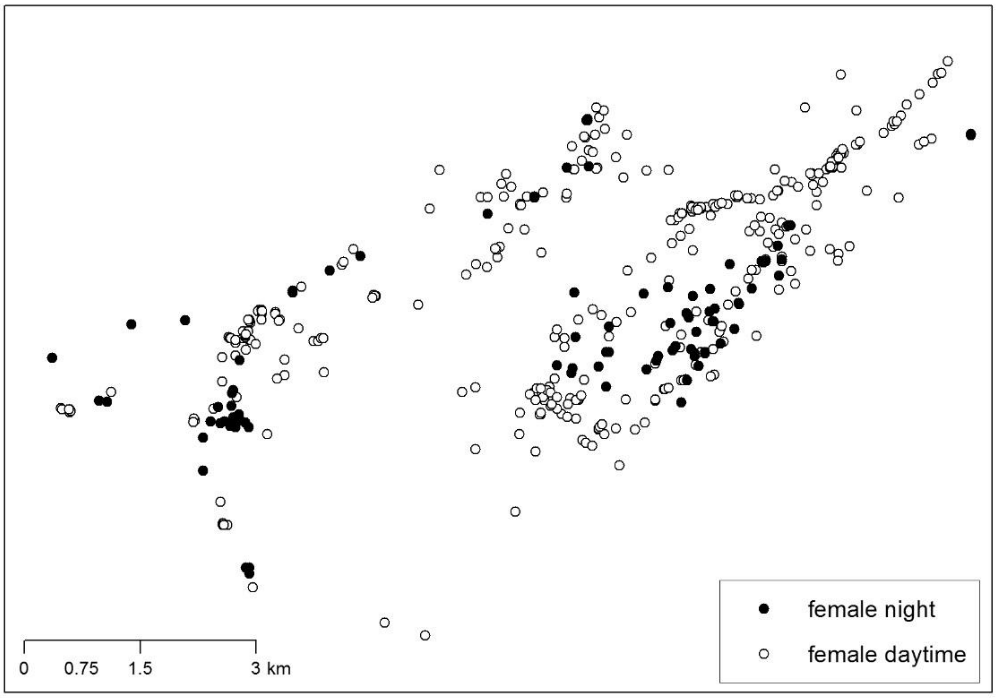

Figure 11. Daytime and night time locations of a female (tag # 49812a) at a post-breeding site, between 30 July and 28 September 2012.

The generally south-eastern direction of post-breeding dispersal (particularly for successful breeders) may be due to several reasons, complementing each other. First, moving south is generally more advantageous as it shortens the distance of subsequent southward migration. Large expanses of dunes and White saxaul *Haloxylon persicum* forest bordering the study site in Bukhara to the south and west (Rachkovskaya 1995) possibly make these compass directions less suitable for the houbara population in the southern Kyzylkum, as negligible numbers of male houbara were detected in unconsolidated sand habitats during the breeding season (Koshkin et al. 2014). This leaves *Artemisia*-dominated steppe-like desert (Rachkovskaya 1995) to the southeast as a more suitable destination for post-breeding dispersal of many individuals, despite the need to cross a wide belt of irrigated farmlands and built-up areas around Bukhara (Fig.12). Indeed, *Artemisia* species are considered to be palatable for the houbara, particularly in autumn and winter (anecdotal information). *Artemisia*-dominated habitats in the southern Kyzylkum were previously found to have consistently higher annual mean NDVI values across years than other shrub assemblages present in the area (C.

Panter, unpublished data). This difference may be due to denser shrub swards typical for *Artemisia*-dominated communities compared to other habitats in the area (Koshkin et al. 2014), and may to some extent explain higher NDVI values for the post-breeding sites. Same general area of tagging and breeding for the majority of tagged birds, as well as the pattern of distribution of human settlements may explain the clustering of many of the post-breeding sites within *Artemisia*-dominated desert (Fig.12). Other birds utilised the edges of arable fields prior to migration, perhaps exploiting similar habitat to that used by houbara during winter in Iran (Aghainajafizadeh et al. 2010). The availability of shade (saxaul plantations used for sand fixation), higher abundance of invertebrates (owing to higher livestock densities) and access to arable (such as alfalfa) crops could potentially attract birds to these areas near irrigation.

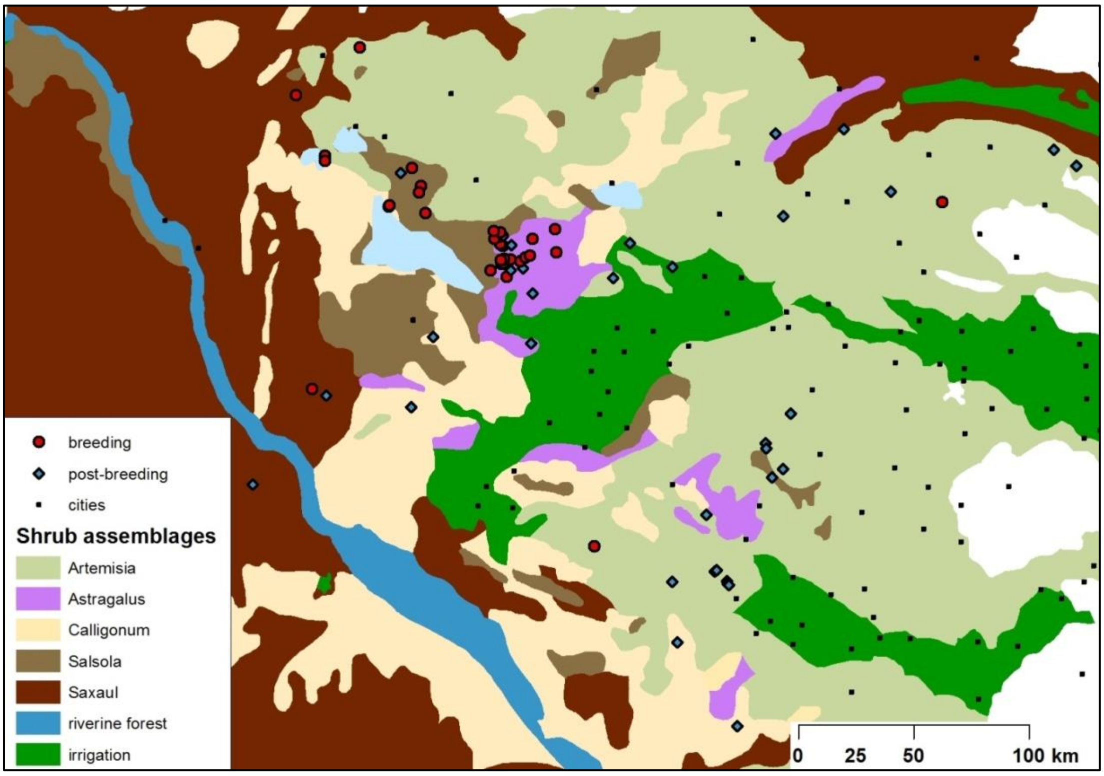

Figure 12. Breeding (display and nesting) and post-breeding home range centroids overlaid on vegetation map produced by Rachkovskaya (1995), reclassified into broad communities by grouping sub-communities with similar dominant perennial shrubs. Small black squares represent city centres (within irrigation zones) or small towns and settlements. This is an example map which shows only a sample of breeding (n = 27) and post-breeding (n = 33) locations.

Why houbara from the study population do not use these potentially more productive areas to breed in the first place remains unclear. *Artemisia*-dominated desert to the southeast is known to support some numbers of breeding houbara (personal observations), but there is no detailed information on densities from these areas. On the other hand, areas adjacent to irrigated fields support low densities of males (Chapter 2) and are unlikely to support many nesting females (Chapter 3) as they are less suitable during the breeding season, most likely due to different shrub assemblages and disturbance from very high livestock densities and people.

Individual variation in space use and movements

Although the majority of birds monitored in this study exhibited similar behaviour, some varied greatly in space use, site fidelity and post-breeding movement patterns. Thus despite a generally high inter-annual site fidelity, two females untypically chose to nest very far from the nest locations of the previous season, although they subsequently returned closer to those initial nest locations. This could be a response to a traumatic experience (trapping) in the preceding year which made them overshoot the 'dangerous' areas on their spring migration and try somewhere new. In the case of the houbara, such a response could be crucial for adult survival, since continuing to nest in an area with a high level of exposure to potential predation (as represented by being caught and fitted with a transmitter) is potentially riskier than moving to a completely new area. However, an alternative explanation is that females simply have very different 'personalities' and thus their behaviour is not uniform. The genetic basis and within-population variance in aspects of avian personality, such as risk-taking behaviour or propensity to investigate novel situations, is becoming more widely appreciated (Réale et al. 2007, Kluen et al. 2012).

The breeding season home ranges of the two 2015 males (Fig.1), are strikingly different from those of the other males, which are compact and centred on core lekking areas. As both these 2015 males were caught and released just before making this uncommon movements, their wider-ranging behaviour could be related to post-catching shock. Both males were caught at seemingly well-established leks (observations of display, presence of feathers, tracks and faeces on leks), so they are unlikely to have been 'floaters' (males not holding a static territory and mobile during the breeding season) (Brown 1969), although the possibility that they were younger males intruding on the lek of a dominant male cannot be excluded. The range of the display period (10 March–11 June, with decline in detectability of display in the latter part of this period) suggests that these two males (trapped on 28 and 30 April respectively) might have been captured after the peak display activity, which could have made them predisposed to abandon their established leks or display activity altogether. At the same time, several other males were caught even later (in the same and different years) but still resumed displaying soon after release, suggesting that age and individuality factors may also have influenced the anomalous 2015 birds.

Analytical challenges

I was not able to use habitat field measurements to conduct analyses of home range habitat selection, as many areas used by birds during the post-breeding and sometimes nesting stages were beyond the extent covered by my fieldwork. I also did not use freely available vegetation and topographic data (such as Landcover, DEM) as preliminary exploration showed that there is very low variation in data to be able to test differences in habitat association between stages.

Further steps and conservation implications

Identification of houbara post-breeding sites is of special importance, as birds were found to rely on resources of these often small areas for several months. With further monitoring of satellite-tagged birds it may be possible to identify general areas where the houbara which breed in the Bukhara study area concentrate during the post-breeding period. Further work is needed to assess habitat and food requirements and threats at the post-breeding sites to understand their importance.

In recent years legal annual quotas issued by local governments to Middle Eastern falconers have permitted autumn hunting of houbara across core breeding areas in Uzbekistan and Kazakhstan. In return, large houbara captive-breeding centres have been built in the areas, mainly aiming to mitigate hunting offtake and support local wild populations by releasing captive-bred birds. My findings show that in the Bukhara region in Uzbekistan, by the time hunting commences (usually September–October), most locally-breeding wild houbara have already left the main hunting areas within the Bukhara concession. Considering only wild birds, this means hunting mostly targets individuals which have moved to the area from elsewhere, probably including long-distance migrants from Kazakhstan or further east. Post release movements of captive bred birds have not yet been compared to post-breeding movements of wild birds. As there is little information on the ratio of hunted wild to captive-bred released birds, it remains unclear which populations are actually hunted and in what proportions, and whether releasing birds of local provenance into the southern Kyzylkum can mitigate the impacts of hunting on other exploited subpopulations.

References

Aghainajafizadeh, S., Hemami, M. R., Karami, M. and Dolman, P. M. 2010. Wintering habitat use by houbara bustard (*Chlamydotis macqueenii*) in steppes of Harat, central Iran. - Journal of Arid Environments 74: 912-917.

Alonso, J. C., Palacin, C., Alonso, J. A. and Martin, C. A. 2009. Post-breeding migration in male great bustards: low tolerance of the heaviest Palaearctic bird to summer heat. - Behavioral Ecology and Sociobiology 63: 1705-1715.

Barron, D. G., Brawn, J. D. and Weatherhead, P. J. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. - Methods in Ecology and Evolution 1: 180-187.

Barta, Z., Mcnamara, J. M., Houston, A. I., Weber, T. P., Hedenstrom, A. and Fero, O. 2008. Optimal moult strategies in migratory birds. - Philosophical Transactions of the Royal Society B-Biological Sciences 363: 211-229.

Bertrand, M. R., Denicola, A. J., Beissinger, S. R. and Swihart, R. K. 1996. Effects of parturition on home ranges and social affiliations of female white-tailed deer. - Journal of Wildlife Management 60: 899-909.

Birdlife International. 2015. Species factsheet: *Chlamydotis macqueenii*. Downloaded from http://www.birdlife.org on 20/10/2015.

Bourass, K. and Hingrat, Y. 2015. Diet of released captive-bred North-African houbara bustards. - European Journal of Wildlife Research 61: 563-574.

Bourass, K., Leger, J. F., Zaime, A., Qninba, A., Rguibi, H., El Agbani, M. A., Benhoussa, A. and Hingrat, Y. 2012. Observations on the diet of the North African houbara bustard during the non-breeding season. - Journal of Arid Environments 82: 53-59.

Brown, J. L. 1969. The buffer effect and productivity in tit populations. - American Naturalist 103: 347-354.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. - Journal of Mammalogy 24: 346-352.

Carroll, M. L., Dimiceli, C. M., Sohlberg, R. A. and Townshend, J. R. G. 2013. 1000m MODIS Normalized Difference Vegetation Index (MOD13A2), Maryland, University of Maryland.

Chappell, A., Seaquist, J. W. and Eklundh, L. 2001. Improving the estimation of noise from NOAA AVHRR NDVI for Africa using geostatistics. - International Journal of Remote Sensing 22: 1067-1080.

Chargé, R., Sorci, G., Saint Jalme, M., Lesobre, L., Hingrat, Y., Lacroix, F. and Teplitsky, C. 2014. Does recognized genetic management in supportive breeding prevent genetic changes in life-history traits? - Evolutionary Applications 7: 521-532.

Combreau, O. and Al Baidhani, M. S. *in litt.* A natural history of the Asian houbara bustard.

Combreau, O., Gelinaud, G. and Smith, T. R. 2000. Home range and movements of houbara bustards introduced in the Najd Pediplain in Saudi Arabia. - Journal of Arid Environments 44: 229-240.

Combreau, O. and Launay, F. 1996. Activity rhythms of houbara bustards (*Chlamydotis undulata macqueenii*) in relation to some abiotic factors. - Journal of Arid Environments 33: 463-472.

Combreau, O., Launay, F., Al Bowardi, M. and Gubin, B. 1999. Outward migration of Houbara Bustards from two breeding areas in Kazakhstan. - Condor 101: 159-164.

Combreau, O., Launay, F. and Lawrence, M. 2001. An assessment of annual mortality rates in adult-sized migrant houbara bustards (*Chlamydotis undulata macqueenii*). - Animal Conservation 4: 133-141.

Combreau, O., Qiao, J., Lawrence, M., Gao, X., Yao, J., Yang, W. and Launay, F. 2002. Breeding success in a Houbara Bustard *Chlamydotis* [*undulata*] *macqueenii* population on the eastern fringe of the Jungar Basin, People's Republic of China. - Ibis 144: E45-E56.

Combreau, O., Riou, S., Judas, J., Lawrence, M. and Launay, F. 2011. Migratory pathways and connectivity in Asian Houbara Bustards: evidence from 15 years of satellite tracking. - PlosOne 6.

De La Morena, E. L. G., Morales, M. B., Bota, G., Silva, J. P., Ponjoan, A., Suarez, F., Manosa, S. and De Juana, E. 2015. Migration patterns of Iberian Little Bustards *Tetrax terax*. - Ardeola 62: 95-112.

Fieberg, J. 2007. Kernel density estimators of home range: Smoothing and the autocorrelation red herring. - Ecology 88: 1059-1066.

Fieberg, J. and Kochanny, C. O. 2005. Quantifying home-range overlap: The importance of the utilization distribution. - Journal of Wildlife Management 69: 1346-1359.

Franklin, J., Duncan, J. and Turner, D. L. 1993. Reflectance of vegetation and soil in Chihuahuan desert plant communities from ground radiometry using SPOT wavebands. - Remote Sensing of Environment 46: 291-304.

Gessner, U., Naeimi, V., Klein, I., Kuenzer, C., Klein, D. and Dech, S. 2013. The relationship between precipitation anomalies and satellite-derived vegetation activity in Central Asia. - Global and Planetary Change 110, Part A: 74-87.

Gintzburger, G., Toderich, K. N., Mardonov, B. K. and Mahmudov, M. M. 2003. Rangelands of the arid and semi-arid zones in Uzbekistan, Paris, CIRAD, ICARDA.

Goward, S. N., Markham, B., Dye, D. G., Dulaney, W. and Yang, J. 1991. Normalized difference vegetation index measurements from the advanced very high resolution radiometer. - Remote Sensing of Environment 35: 257-277.

Gubin, B. M. 2004. Drofa-krasotka (Asian Houbara) (in Russian), Almaty Kolor.

Hakkarainen, H., Ilmonen, P., Koivunen, V. and Korpimäki, E. 2001. Experimental increase of predation risk induces breeding dispersal of Tengmalm's owl. - Oecologia 126: 355-359.

Hingrat, Y., Jalme, M. S., Chalah, T., Orhant, N. and Lacroix, F. 2008. Environmental and social constraints on breeding site selection. Does the exploded-lek and hotspot model apply to the Houbara bustard *Chlamydotis undulata undulata*? - Journal of Avian Biology 39: 393-404.

Hingrat, Y., Jalme, M. S., Ysnel, F., Lacroix, F., Seabury, J. and Rautureau, P. 2004. Relationships between home-range size, sex and season with reference to the mating system of the Houbara Bustard *Chlamydotis undulata undulata*. - Ibis 146: 314-322.

Höfle, U., Millán, J., Gortázar, C., Buenestado, F. J., Marco, I. and Villafuerte, R. 2004. Self-injury and capture myopathy in net-captured juvenile red-legged partridge with necklace radiotags. - Wildlife Society Bulletin 32: 344-350.

Hoover, J. P. 2003. Decision rules for site fidelity in a migratory bird, the prothonotary warbler. - Ecology 84: 416-430.

Islam, M. Z., Basheer, M. P., Shah, M. S., Al Subai, H. and Boug, A. 2012a. Captive-breeding and reintroduction of the Asian Houbara Bustard *Chlamydotis macqueenii* in the Kingdom of Saudi Arabia: lessons learned. - International Zoo News 59: 338-360.

Islam, M. Z., Singh, A., Basheer, M. P., Judas, J. and Boug, A. 2012b. Differences in space use and habitat selection between captive-bred and wild-born houbara bustards in Saudi Arabia: results from a long-term reintroduction program. - Journal of Zoology 289: 251-261.

IUCN. 2015. The IUCN Red List of Threatened Species.Version 2015-3. http://www.iucnredlist.org downloaded on 05/10/2015.

Jahn, A. E., Cueto, V. R., Sagario, M. C., Mamani, A. M., Vidoz, J. Q., De Casenave, J. L. and Di Giacomo, A. G. 2009. Breeding and winter site fidelity among eleven neotropical austral migrant bird species. - Ornitologia Neotropical 20: 275-283.

Judas, J., Combreau, O., Lawrence, M., Saleh, M., Launay, F. and Gao, X. Y. 2006. Migration and range use of Asian Houbara Bustard *Chlamydotis macqueenii* breeding in the Gobi Desert, China, revealed by satellite tracking. - Ibis 148: 343-351.

Keating, K. A. and Cherry, S. 2009. Modeling utilization distributions in space and time. - Ecology 90: 1971-1980.

Kessler, A. E., Batbayar, N., Natsagdorj, T., Batsuur', D. and Smith, A. T. 2013. Satellite telemetry reveals long-distance migration in the Asian great bustard *Otis tarda dybowskii*. - Journal of Avian Biology 44: 311-320.

Kie, J. G., Bowyer, R. T., Nicholson, M. C., Boroski, B. B. and Loft, E. R. 2002. Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. - Ecology 83: 530-544.

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., Gaillard, J. M. and Moorcroft, P. R. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? - Philosophical Transactions of the Royal Society B-Biological Sciences 365: 2221-2231.

Klaassen, R. H. G., Hake, M., Strandberg, R., Koks, B. J., Trierweiler, C., Exo, K.-M., Bairlein, F. and Alerstam, T. 2014. When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. - Journal of Animal Ecology 83: 176-184.

Kluen, E., Kuhn, S., Kempenaers, B. and Brommer, J. E. 2012. A simple cage test captures intrinsic differences in aspects of personality across individuals in a passerine bird. - Animal Behaviour 84: 279-287.

Koshkin, M. A., Collar, N. J. and Dolman, P. M. 2014. Do sheep affect distribution and habitat of Asian Houbara *Chlamydotis macqueenii*? - Journal of Arid Environments 103: 53-62.

Lapiedra, O., Ponjoan, A., Gamero, A., Bota, G. and Manosa, S. 2011. Brood ranging behaviour and breeding success of the threatened little bustard in an intensified cereal farmland area. - Biological Conservation 144: 2882-2890.

Laver, P. N. and Kelly, M. J. 2008. A critical review of home range studies. - The Journal of Wildlife Management 72: 290-298.

Maloney, R. F. 2003. Survival, breeding and movements of reintroduced Asiatic Houbara (*Chlamydotis [undulata] macqueenii*) in Mahazat as-Sayd reserve, Saudi Arabia. University of New England.

Meszaros, A. L., Kajdocsi, S., Szentirmai, I., Komdeur, J. and Szekely, T. 2006. Breeding site fidelity in penduline tit *Remiz pendulinus* in Southern Hungary. - European Journal of Wildlife Research 52: 39-42.

Mitchell, G. W., Taylor, P. D. and Warkentin, I. G. 2010. Assessing the function of broad-scale movements made by juvenile songbirds prior to migration. - Condor 112: 644-654.

Murray, D. L. and Fuller, M. R. 2000. A critical review of the effects of marking on the biology of vertebrates. In: Boitani, L. and Fuller, T. K. (eds.) Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, pp. 15-64.

Paradis, E., Baillie, S. R., Sutherland, W. J. and Gregory, R. D. 1998. Patterns of natal and breeding dispersal in birds. - Journal of Animal Ecology 67: 518-536.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. J. and Stenseth, N. C. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. - Trends in Ecology & Evolution 20: 503-510.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, URL http://www.R-project.org/. Vienna, Austria.

Rachkovskaya, E. I. 1995. Vegetation map of Kazakhstan and Middle Asia (Desert region). Russian Academy of Sciences, Saint Petersburg.

Réale, D., Reader, S. M., Sol, D., Mcdougall, P. T. and Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. - Biological Reviews 82: 291-318.

Riou, S. and Combreau, O. 2014. Male territories and the lek-like mating system of MacQueen's Bustard *Chlamydotis macqueenii*. - Journal of Ornithology 155: 959-967.

Riou, S., Judas, J., Lawrence, M., Pole, S. and Combreau, O. 2011. A 10-year assessment of Asian Houbara Bustard populations: trends in Kazakhstan reveal important regional differences. - Bird Conservation International 21: 134-141.

Saint Jalme, M. and Van Heezik, Y. 1995. Propagation of the Houbara Bustard*,* London, Keegan Paul International.

Sara, M., Campobello, D., Zanca, L. and Massa, B. 2014. Food for flight: pre-migratory dynamics of the Lesser Kestrel *Falco naumanni*. - Bird Study 61: 29-41.

Schlossberg, S. 2009. Site fidelity of shrubland and forest birds. - Condor 111: 238-246.

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J. and Gitzen, R. A. 1999. Effects of sample size on kernel home range estimates. - The Journal of Wildlife Management 63: 739-747.

Seaman, D. E. and Powell, R. A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. - Ecology 77: 2075-2085.

Silva, J. P., Faria, N. and Catry, T. 2007. Summer habitat selection and abundance of the threatened little bustard in Iberian agricultural landscapes. - Biological Conservation 139: 186-194.

Silverman, B. W. 1986. Density estimation for statistics and data analysis*.*, London, Chapman and Hall.

Spraker, T. R., Adrian, W. J. and Lance, W. R. 1987. Capture myopathy in wild turkeys (*Meleagris gallopavo*) following trapping, handling and transportation in Colorado. - Journal of Wildlife Diseases 23: 447-453.

Terraube, J., Mougeot, F., Cornulier, T., Verma, A., Gavrilov, A. and Arroyo, B. 2012. Broad wintering range and intercontinental migratory divide within a core population of the near-threatened pallid harrier. - Diversity and Distributions 18: 401-409.

Tigar, B. J. and Osborne, P. E. 2000. Invertebrate diet of the Houbara Bustard *Chlamydotis undulata macqueenii* in Abu Dhabi from calibrated faecal analysis. - Ibis 142: 466-475.

Todd, L. D., Poulin, R. G., Brigham, R. M., Bayne, E. M. and Wellicome, T. I. 2007. Pre-migratory movements by juvenile burrowing owls in a patchy landscape. - Avian Conservation and Ecology 2.

Tomkiewicz, S. M., Fuller, M. R., Kie, J. G. and Bates, K. K. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. - Philosophical Transactions of the Royal Society B-Biological Sciences 365: 2163-2176.

Tourenq, C., Combreau, O., Lawrence, M., Pole, S. B., Spalton, A., Gao, X. J., Al Baidani, M. and Launay, F. 2005. Alarming houbara bustard population trends in Asia. - Biological Conservation 121: 1-8.

Villers, A., Millon, A., Jiguet, F., Lett, J.-M., Attie, C., Morales, M. B. and Bretagnolle, V. 2010. Migration of wild and captive-bred Little Bustards *Tetrax tetrax*: releasing birds from Spain threatens attempts to conserve declining French populations. - Ibis 152: 254-261.

Viter, S. G. 2013. Nest site fidelity and occupancy in birds of prey (*Falconiformes*) in specially protected and unprotected areas of eastern Ukraine. - Russian Journal of Ecology 44: 36-42.

Weiss, J. L., Gutzler, D. S., Coonrod, J. E. A. and Dahm, C. N. 2004. Long-term vegetation monitoring with NDVI in a diverse semi-arid setting, central New Mexico, USA. - Journal of Arid Environments 58: 249-272.

Willemoes, M., Strandberg, R., Klaassen, R. H. G., Tøttrup, A. P., Vardanis, Y., Howey, P. W., Thorup, K., Wikelski, M. and Alerstam, T. 2014. Narrow-front loop migration in a population of the common cuckoo *Cuculus canorus*, as revealed by satellite telemetry. - PlosOne 9: e83515.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. - Ecology 70: 164-168.

Chapter 6 – Discussion

Key findings

This study attempted to improve our understanding of aspects of the species-habitat relationship, abundance and productivity of Asian houbara *Chlamydotis macqueenii* in Uzbekistan. The following key evidence is provided in this thesis:

Contrary to expectations, there appeared to be no negative landscape-scale association between livestock density and the abundance and/or distribution of male houbara. This finding is consistent with the lack of a marked effect of livestock on desert shrub vegetation structure and composition (Chapter 2).

Chapter 3 showed that habitat characteristics selected by males at the landscape scale were more likely to maximise visibility and performance of their displays, with male houbara numbers found to be greater with lower mean shrub height, more gravel and flatter terrain. For the first time, abundance of the Asian houbara was related to particular plant assemblages and the first robust estimate of local density and regional population size was obtained.

It has also been shown that houbara nesting success was unaffected by variation in shrub species composition or livestock density, but nests placed within taller vegetation experienced greater success. Surprisingly, Desert monitor *Varanus griseus,* rather than fox *Vulpes* spp., was identified as the main predator of houbara nests; and earlier clutches were found to have higher success owing to the emergence of this lizard later in the season (Chapter 4).

Houbara breeding and post-breeding space use and movements were quantified and are now better understood. Satellite-tracking revealed high site-fidelity of males to their display sites and intra-seasonal fidelity of females to breeding areas. During the post-breeding period (during moult, prior to migration) adult birds were found to be using completely different areas than their breeding season range, which has not been previously reported for the species. These areas were found to be more productive in terms of vegetation compared to breeding sites (Chapter 5).

In this concluding chapter I discuss potential implications of these key research findings for the conservation and management of the houbara population in the Kyzylkum, in the hope that knowledge and recommendations resulting from this work may be relevant to other houbara populations and other study systems. Finally I discuss priorities for further research and questions remaining to be addressed.

Houbara and habitat

Habitat is key in providing an animal with food, breeding sites and shelter from both weather and predators. Some animals have very specific habitat requirements, and are therefore very vulnerable if such habitat is damaged or depleted (Fuller 2012); on the other hand, other species are more generalist in their requirements and are able to utilise a range of habitats (Barnagaud et al. 2011, Dennis et al. 2011). Long-distance migrants and species occupying temperate lower-productivity environments are predicted to be more generalist owing to reduced feasibility of niche specialisation.

Habitat effects on breeding houbara

Unsurprisingly, breeding male Asian houbaras were found in higher numbers in areas with shorter shrub sward at the landscape scale (Chapter 3). The lek system assumes mutual visibility of nearby males when they form display clusters; and in the classic lek system males can be separated by only few metres during display (Bradbury 1981). Some species, however, form 'exploded' leks, where, even when males aggregate in a suitable display habitat, each male can have a relatively large territory (Hoglund and Alatalo 1995). Such a lek system is reported for the African houbara (Hingrat et al. 2008) and is thought to be common among other bustard species (Jiguet et al. 2000). In a loose, 'lek-like' distribution of male Asian houbara (Riou and Combreau 2014), males display at distances of 1.5 km (or greater) from each other. However at such distances, even being very obvious in its display, a male houbara very likely has lower chances of being spotted by another male or a potential mate when surrounded by shrubs taller than the bird itself, especially in a predominantly flat landscape.

Males were also found to be selecting flat areas, as opposed to undulated topography or areas intersected by valleys and wadis. This may well be linked to a general preference for flat terrain by a species which spends most of its life walking or running, with additional benefits of an unhindered view of an approaching threat during breeding, when individuals are most vulnerable. At the same time, even in flat areas males were often observed displaying on slight elevations (personal observations), when available, which can greatly increase the visibility of their display. Therefore it is likely that, to have optimal conditions for the display itself as well as the largest display visibility radius, male houbara may select not only open, less vegetated lek sites (ideally elevated), but also shorter mean vegetation and flatter terrain at the scale of the surrounding landscape.

Male houbara densities in the southern Kyzylkum differed between the four habitats considered, with highest densities supported by *Salsola rigida,* followed by *S. arbuscula* and *Astragalus* shrub assemblages (Chapter 3). It is possible that, at the scale of different habitats and parts of landscape, the lower suitability of *Calligonum* and *Artemisia* shrub assemblages for breeding females may affect male densities in these areas, which could indicate that males lek where females congregate for resources (the 'hotspot' model of lek development: Beehler and Foster 1988). However, owing to lower sampling effort, no nests were found in the *Calligonum* shrub assemblage and very few in the *Artemisia* shrub assemblage (Chapters 4), so this remains a speculation.

On the other hand, the very strong inter-annual display site fidelity of males and weaker inter-annual fidelity of females suggest that male distribution at a more local scale is maybe more static than female nest site selection, which aligns more with the 'hotshot' model of lek development (Beehler and Foster 1988). This model suggests that, in species with a mating system not based on resources, certain males are more successful in attracting mates, with other, less successful males clustering around to attempt to 'steal' matings. However, this model was considered improbable by Riou and Combreau (2014) after they found that six broods hatched within the same area (approx. 100 km^2) were sired by at least five different males. These authors also speculated that the absence of a typical lek *per se* may potentially be due to a lack of variation in the quality of males with fixed territories, meaning that females do not have strong preferences for particular phenotypes, but that fixed (mature, dominant) males may be more attractive to females than floaters that display next to fixed males in an attempt to gain matings (Riou and Combreau 2014).

Owing to their cryptic behaviour it was not possible to explore habitat influences on female abundance and distribution, but it was still possible to test for the effects of habitat on nesting success. In contrast to the males' selection of short vegetation for display, the higher success of females nesting in areas with taller mean shrub height (within radius of 50 m around nests) suggests that they may benefit from concealment by shrubs, as a strategy to avoid nest predation.

Post-breeding habitat use

After the completion of breeding both males and females moved to new sites, often located >100 km from their breeding sites, subsequently staying there for months before embarking on a long journey to the wintering grounds. Such a pronounced differentiation between breeding and post-breeding space use seems to be a characteristic of migratory but not of resident populations of Asian houbara; indeed, it has not previously been reported and quantified for either the African or for the Asian species. As findings presented earlier (Chapter 5) suggest, habitat is likely to play a crucial role in the selection of these sites by providing shade, shelter and food at levels which breeding sites are possibly unable to provide during summer–autumn period.

Asian houbara is a long-distance migrant, with birds from the southern Kyzylkum covering up to 1,300 km (R. Burnside personal comments) and birds from China up to 4,000 km (Judas et al. 2006, Combreau et al. 2011) to reach their wintering grounds. Satellite tracking of houbara suggests that some individuals are able to cover long distances in a short time. For example, one male tracked during his southern migration from the breeding grounds in China covered over 4,000 km in 13 days, travelling on average 318 km per day (Judas et al. 2006). At the same time, data from our study area show a relatively short migratory route and slow migration, with mean number of days spent on stopover sites exceeding number of days spent on the move (R. Burnside unpublished data). Therefore it is possible to conclude that the transitory stage between houbara breeding and migration could be a crucial stage for recovery after energy-demanding breeding, moult and survival through probably the toughest period of the year, rather than solely a fuelling pre-migratory stage. As mean summer maximum temperatures are comparable to those in other parts of the species range, such as western Kazakhstan or China, similar pattern of post-breeding space use is likely for other populations of Asian houbara.

Desert generalist specialist

Dennis et al. (2011) defines ecological specialism/generalism 'as a gradient in resource use, specialism describing use of limited (typically one to few related) resource components and generalism numerous (many/varied, more distantly related) components'. Same authors state that generalism is a common feature of nature and that specialisation is not a necessary or sole condition for speciation. Generalism can also be considered important in an evolutionary context (i.e. gene selection, extinction avoiding), as opposed to specialization, which tends to be associated with extinction with its vulnerable niche and resource links (McKinney 1997). Others, however doubt whether generalism truly occurs in nature (Loxdale et al. 2011).

Findings presented earlier suggest that the Asian houbara is a versatile, adaptable occupant of a range of desert habitats. Desert heterogeneity at local and landscape scales provides the necessary variation in habitat structure, with requirements differing with sex (display or nesting) and through the season (breeding or post-breeding). The vegetation communities considered seem to provide a broadly similar range of resources and shelter. However, despite being a generalist in using different habitat types, the houbaras breeding in the southern Kyzylkum seem to disfavour vegetation with more extreme heights, i.e. taller (*Calligonum* and Saxaul) or much shorter (*Artemisia*) (Chapter 2 and 3). Such avoidance may be explained not only by disadvantages related to structure of these habitats (i.e. limited visibility in tall shrubs, high exposure to a threat in short homogeneous vegetation), but also by the relative abundance they hold of invertebrates and palatable plant species.

High breeding site fidelity suggests that migratory Asian houbara are likely to breed in the same general area (approx. 50 km^2) from year to year. However, the evidence of post-breeding movements, annual migrations and pre-breeding juvenile dispersal suggest that over the course of a year houbaras occupy sometimes strikingly different habitats. Alongside the huge range of the species, spanning different ecosystems, each characterised by different plant communities with different structures and levels of heterogeneity (Olson 2001), this either suggests the high level of adaptability of the species or that the condition it needs can be provided in a wide range of environmental settings.

This study provides strong evidence that Asian houbara productivity and abundance do not vary greatly among suitable habitats. Therefore, there are no obvious *in-situ* measures which could be implemented to increase productivity of the local wild population through habitat management.

Houbara and pastoralism

The main parties involved in the houbara breeding and introduction program in Uzbekistan recently viewed pastoralism as a probable threat to both the integrity of the desert habitats and thus to houbara populations. Local pastoralists (particularly owners of private livestock) are marginalised in terms of welfare, livelihoods and opportunity, and so would be potentially vulnerable if there was a conflict of interest between them and economic interest of either the government or other powerful and influential stakeholders. Before the onset of the current study, the possibility existed that the initiators of the captive breeding program, with governmental support, could seek to relocate many pastoralists from substantial areas of the concession in order to 'improve' houbara habitat. A similar measure was previously used in Mahazat as-Sayd Protected Area in Saudi Arabia, largely managed for houbara re-introduction. After receiving protected status the reserve (around 2,200 km^2) was fenced, partly to prevent access for livestock (Combreau et al. 2000). Although in Saudi Arabia this might have been a necessary measure, as the surrounding desert was described as severely overgrazed, in our study area grazing was not found to have adverse effects on desert vegetation or on houbara.

Overgrazing remains an issue in Uzbekistan in the near vicinity of settlements, wells and other water sources, which represent areas of high and long-term concentrations of livestock (Rajabov 2009, Koshkin et al. 2014). However, at the scale of the desert landscape such localised damage to desert vegetation does not appear to extend far enough to degrade habitat quality for houbara, at least in part owing to the decay of the old Soviet infrastructure. Excluding sheep from traditional grazing areas would possibly force their owners to use other less suitable pastures and probably have unpredictable effects on pastoralist livelihoods and local desert, both in the exclusion zone and in livestock relocation areas. The evidence this study provides should prevent potential conflict between houbara management and local pastoralist communities and help avoid potential detrimental effects on local desert.

A potentially more important current threat to the local desert ecosystem is from fuelwood collection and the uprooting of shrubs for winter fodder and silkworm industry, which may have serious detrimental effects on vegetation structure (Gintzburger et al. 2003, personal observations). Uprooting of larger shrubs (to remove the thicker, denser roots) for fuelwood by local villagers and the collection of smaller shrubs (such as *Astragalus* spp.) for use as structure for silkworm cocoons, together with the high grazing density of livestock, has potentially caused the destabilisation of sands around irrigation areas in the Bukhara region. A large proportion of these areas, previously classified as *Astragalus*-dominated habitats (Rachkovskaya 1995), seems to have been replaced in the last 20–30 years by psammophytic vegetation on unconsolidated sands, with areas of shifting dunes (Koshkin et al. 2014).

In the deserts and semi-deserts of Central Asia both vegetation and houbara historically have co-existed with different densities of grazing animals. Throughout the Holocene and until recently these areas were grazed by herds of Goitered gazelle *Gazella subgutturosa*, Asiatic wild ass *Equus hemionus* and Przewalski's horse *Equus przewalski* (Bahloul et al. 2001). Pastoralism probably arrived in the Kyzylkum desert approximately 8,000 years ago with the first settlers (Vinogradov and Mamedov 1975, Harris et al. 2010), with sheep and goat gradually occupying the niche of widely persecuted wild grazers (Wright et al. 2012). Today many pastoralists in Uzbekistan follow transhumance systems of rangeland use, timing their movements by the seasons and according to the availability of fodder and water (Gintzburger et al. 2003). In spring sheep and goats graze ephemeral vegetation in sandy desert, in summer they are driven to higher ground (where possible) or areas adjacent to water sources, and moved back to sandy and clay desert to feed on dry ephemerals and perennial shrubs in winter (personal observations). Such systems of seasonal movements and rotation of pastures seem to have no major adverse effect on desert vegetation at the landscape scale. At the same time there is a gradient of livestock grazing densities across the study area, with higher stocking rates on desert pastures adjacent to densely populated irrigated areas, water sources or settlements scattered throughout the desert, and low livestock densities across large, usually more remote territories (Koshkin et al. 2014).

Kazakhstan is thought to support the largest part of the Asian houbara breeding population (over 60%), followed by Uzbekistan, Mongolia and China (BirdLife International 2014). As in the southern Kyzylkum, the distribution of the human population in the deserts of Kazakhstan is limited by scarce water sources. The spatial pattern of grazing densities reported for the desert and semi-desert areas of south-eastern Kazakhstan seems to be similar to that currently observed in our study area, with the majority of livestock kept in proximity to human habitation, causing localised overgrazing, and smaller numbers of livestock distributed across vast expanses of the surrounding desert (Kerven et al. 2006). Parts of the houbara range in Mongolia and China are also known to be used by seasonal pastoralists, often represented by large Kazakh minorities residing in these areas (Hamann 1999). Therefore a similar compatibility of houbara populations with moderate grazing regimes is likely for most of the species' breeding range across Central Asia, with similar grazing systems, environmental conditions and cultural background.

There seems to be no current need for targeted habitat management with respect to pastoralism, at least in the southern Kyzylkum desert. The results of this study provide strong evidence that at the scale of the study area houbara and moderate-intensity pastoralism can peacefully coexist.

Consequences of findings

In-situ conservation

The only practical population management measure which currently appears to be obvious, considering the findings presented above, is the control of monitor lizards. However, this measure should not be advocated due to several reasons. First of all, despite the relatively long period (four years) the study covers, it remains unclear whether monitors are the only significant predators of houbara clutches and broods in this part of the Kyzylkum desert. Rodent population depression (i.e. from a peak in 2010 to crash in 2012) coincided with the start of the period covered by this study and may have adversely affected (Steen et al. 1990, Hanski et al. 2001) numbers of foxes, one of the main predators of houbara nests elsewhere and a possible predator of young (5–6 months old) desert monitors emerging in spring (Pianka et al. 2004). At the same time, rodents may represent a substantial part of the desert monitor's diet, depending on the region (Pianka et al. 2004). As the dietary preferences of monitors were often reported to reflect relative abundance of prey species (Pianka et al. 2004), in the absence of rodents monitors are likely to prey more on bird eggs and invertebrates, so there is a possibility that the predation of houbara nests will be minimal once rodent numbers are high again. Therefore further research covering years of high rodent and fox populations is required before the consequences of predator communities for houbara productivity can be fully understood. Second, there is a lack of data on the distribution and population size of desert monitor, and although its status has not yet been assessed by IUCN (IUCN 2015), this species is included in CITES Appendix I (species threatened with extinction, trade being permitted only in exceptional circumstances), and it has been listed in Red Data books of several range countries. Third, predator controls are not always successful in increasing bird breeding populations in the long term (Côté and Sutherland 1997), while the ecological consequences of removing one of the desert's top predators are likely to have unpredictable impacts on the local ecosystem through potential effects on trophic cascades (Hebblewhite et al. 2005).

Knowledge of the Asian houbara's population size and trends over time is a basic requirement for conservation and management programs. Numbers may change owing to adverse anthropogenic causes or fluctuate naturally in response to environmental factors or density-dependent effects of population level itself (Bibby et al. 1992). One of the key contributions of this research towards the sustainable management of local houbara populations is the establishment of a robust census methodology and the first robust density estimates, with population assessments conducted in 2013 across the whole study area and repeated annually thereafter. Such baseline estimate of the local population size and a repeatable census technique adapted to local conditions will be important for population monitoring and management.

Captive breeding

Habitat conditions at post-release sites are presumed to be crucial for the survival of captive-bred released birds. Habitat heterogeneity in the southern Kyzylkum desert seems to create suitable conditions for breeding wild houbara across a range of distinct habitats. This could potentially mean that: (i) for a generalist species like houbara there is no lack of suitable breeding habitat in the area; and (ii) wild houbara populations in the area are doing well, at least in terms of nesting productivity and male breeding densities. Therefore, considering the numerous risks and uncertainty of the effectiveness of the local captive-breeding program in sustaining the local population through mitigation of local hunting off-take (Burnside *in litt.*), it seems that the sustainable use of the local wild population, with few management interventions required other than the exercise of quotas, could be a better conservation solution than the *ex-situ* measures. Although subject to local plant species, similar heterogeneous habitats have been reported for Asian houbara breeding sites throughout its range (Launay et al. 1997, Yang et al. 2002, Gubin 2004, Judas et al. 2006, Aghanajafizadeh et al. 2012, Islam et al. 2012). There is therefore great potential for population recoveries throughout the species' range, at least when habitat is concerned.

Further research, next steps and interesting questions remaining

Findings reported and discussed above do not point to any obvious and straightforward *in situ* measures for the mitigation of the currently unsustainable Asian houbara hunting off-take, at least at the scale of the southern Kyzylkum and probably across most of the Central Asian range of the species. This means that limited and sustainable hunting quotas both at breeding and wintering sites, based on robust estimates of local houbara population demography (incorporating productivity, neonatal first winter and adult survival estimates) and supported by effective 'on the ground' regulation, remain the most immediate and appropriate solution. However, a number of important questions still remain before this solution can be successfully implemented, and to answer them several key steps need to be taken.

First of all it is necessary to identify what level of hunting off-take (if any) would be sustainable for a given population. To know this, one needs to establish a demographic trend for such a population. Estimates of annual nesting productivity of Asian houbara obtained during this study are important for estimating the survival of the population, but such estimation is not possible without data on juvenile and adult survival, which should be the next important targets of research.

Second, it is currently unknown which breeding subpopulations are exploited during the autumn hunt in the southern Kyzylkum. It was shown above that after breeding the majority of adult birds move to different sites outside (SE of) the hunting concession, where they spend the time remaining until they begin migration. It is also known that at least some of these areas are used by houbara when breeding. If such post-breeding movements are typical also for other populations, one would expect houbara breeding further north to undertake similar movements and use breeding areas of a given population as post-breeding sites. As juveniles were not found to follow adults to post-breeding sites (R. Burnside unpublished data), it remains unknown what proportion of the hunted birds are recruits from the local breeding population (i.e. first-winter birds) and what is the contribution of northern breeders to the hunting bag. Anecdotal evidence suggests that at least a proportion of birds present in the Bukhara region during the hunt may originate from populations further north, as in one of three birds caught there during the hunt and one of two birds caught in December bred in Kazakhstan the following spring.

Third, post-breeding requirements of the local houbara population should be assessed to understand which factors explain their choice of post-breeding sites. For example, moulting during this period may suggest these sites may be particularly remote from potential predators; hence estimates of predator densities compared to those at the breeding sites could be important. Assessment of habitat structure at post-breeding sites may also clarify whether houbara need taller shrubs for shade and denser vegetation for cover.

Furthermore, there are currently very limited data on the survival, space use and movements of wild juveniles, as they are very difficult to catch, with their weight and size limiting use of satellite transmitters. Although to reach a reasonable sample size several more years of catching and tagging will be required, this information will be extremely valuable for the estimation of overall survival. Additionally, an assessment of the habitat requirements of juvenile houbaras might help to improve post-release and winter survival of captive-bred birds, which are usually released as juveniles.

Finally, if the captive-breeding program is to continue, managers need to decide whether captive breeding is to be used as a tool for complementing the productivity of the wild population (through releasing enough captive-bred birds to survive to replace hunted wild adults) or for minimising the impact on the wild population by releasing captive-bred birds into the desert as substitute quarry.

References

Aghanajafizadeh, S., Hemami, M. R. and Heydari, F. 2012. Nest-site selection by the Asian Houbara Bustard, *Chlamydotis macqueenii*, in the steppe of Harat, Iran (Aves: Otidae). - Zoology in the Middle East 57: 11-18.

Bahloul, K., Pereladova, O. B., Soldatova, N., Fisenko, G., Sidorenko, E. and Sempere, A. J. 2001. Social organization and dispersion of introduced kulans (*Equus hemionus kulan*) and Przewalski horses (*Equus przewalski*) in the Bukhara Reserve, Uzbekistan. - Journal of Arid Environments 47: 309-323.

Barnagaud, J. Y., Devictor, V., Jiguet, F. and Archaux, F. 2011. When species become generalists: on-going large-scale changes in bird habitat specialization. - Global Ecology and Biogeography 20: 630-640.

Beehler, B. M. and Foster, M. S. 1988. Hotshots, hotspots, and female preference in the organization of lek mating systems. - The American Naturalist 131: 203-219.

Bibby, C. J., Burgess, N. D. and Hill, D. A. 1992. Purpose and design in counting birds. In: Bibby, C. J. and Hill, N. D. B. A. (eds.) Bird census techniques. Academic Press, Boston, pp. 1-23.

Birdlife International. 2014. Review of the global conservation status of the Asian Houbara Bustard *Chlamydotis macqueenii*. Report to the Convention on Migratory Species Office – Abu Dhabi, Cambridge, UK, BirdLife International.

Bradbury, J. W. 1981. The evolution of leks. In: Alexander, R. D. and Tinkle, D. W. (eds.) Natural selection and social behaivior: Research and new theory. Chiron Press, New York, pp. 138-169.

Burnside, R. J. *in litt.* How can captive breeding best help conserve the overexploited Asian Houbara *Chlamydotis macqueenii*? - Ibis *submited on 31.07.2015.*

Combreau, O., Gelinaud, G. and Smith, T. R. 2000. Home range and movements of houbara bustards introduced in the Najd Pediplain in Saudi Arabia. - Journal of Arid Environments 44: 229-240.

Combreau, O., Riou, S., Judas, J., Lawrence, M. and Launay, F. 2011. Migratory pathways and connectivity in Asian Houbara Bustards: evidence from 15 years of satellite tracking. - PlosOne 6.

Côté, I. M. and Sutherland, W. J. 1997. The effectiveness of removing predators to protect bird populations. - Conservation Biology 11: 395-405.

Dennis, R. L. H., Dapporto, L., Fattorini, S. and Cook, L. M. 2011. The generalism-specialism debate: the role of generalists in the life and death of species. - Biological Journal of the Linnean Society 104: 725-737.

Fuller, R. J. (ed.) 2012. Birds and habitat: Relationships in changing landscapes, Cambridge University Press, Cambridge, UK.

Gintzburger, G., Toderich, K. N., Mardonov, B. K. and Mahmudov, M. M. 2003. Rangelands of the arid and semi-arid zones in Uzbekistan, Paris, CIRAD, ICARDA.

Gubin, B. M. 2004. Drofa-krasotka (Asian Houbara) (in Russian), Almaty Kolor.

Hamann, B. 1999. Impacts of the reform policy on Kazakh pastoral farming in China - a survey carried out along the Southern Border of the Dsungarian Basin/Xinjiang. - Geographische Zeitschrift 87: 46-53.

Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L. and Turchin, P. 2001. Small-rodent dynamics and predation. - Ecology 82: 1505-1520.

Harris, D. R., Asouti, E., Bogaard, A., Charles, M., Conolly, J., Coolidge, J., Dobney, K., Gosden, C., Heathcote, J., Jaques, D., Larkum, M., Limbrey, S., Meadows, J., Schlanger, N. and Wilkinson, K. 2010. Origins of agriculture in western Central Asia: An environmental-archaeological study, University of Pennsylvania Press.

Hebblewhite, M., White, C. A., Nietvelt, C. G., Mckenzie, J. A., Hurd, T. E., Fryxell, J. M., Bayley, S. E. and Paquet, P. C. 2005. Human activity mediates a trophic cascade caused by wolves. - Ecology 86: 2135-2144.

Hingrat, Y., Jalme, M. S., Chalah, T., Orhant, N. and Lacroix, F. 2008. Environmental and social constraints on breeding site selection. Does the exploded-lek and hotspot model apply to the Houbara bustard *Chlamydotis undulata undulata*? - Journal of Avian Biology 39: 393-404.

Hoglund, J. and Alatalo, R. V. 1995. Leks*,* Princeton, New Jercey, Princeton University Press.

Islam, M. Z., Singh, A., Basheer, M. P., Judas, J. and Boug, A. 2012. Differences in space use and habitat selection between captive-bred and wild-born houbara bustards in Saudi Arabia: results from a long-term reintroduction program. - Journal of Zoology 289: 251-261.

IUCN. 2015. The IUCN Red List of Threatened Species.Version 2015-3. http://www.iucnredlist.org downloaded on 05/10/2015.

Jiguet, F., Arroyo, B. and Bretagnolle, V. 2000. Lek mating systems: a case study in the Little Bustard *Tetrax tetrax*. - Behavioural Processes 51: 63-82.

Judas, J., Combreau, O., Lawrence, M., Saleh, M., Launay, F. and Gao, X. Y. 2006. Migration and range use of Asian Houbara Bustard *Chlamydotis macqueenii* breeding in the Gobi Desert, China, revealed by satellite tracking. - Ibis 148: 343-351.

Kerven, C., Shanbaev, K., Alimaev, J., Smailov, A. and Smailov, K. 2006. Livestock mobility and degradation in Kazakhstan's semi-arid rangelands. In: Behnke, R. (ed.) Socio-economic causes and consequences of desertification in Central Asia. Springer, Dordrecht, pp. 113-140.

Koshkin, M. A., Collar, N. J. and Dolman, P. M. 2014. Do sheep affect distribution and habitat of Asian Houbara *Chlamydotis macqueenii*? - Journal of Arid Environments 103: 53-62.

Launay, F., Roshier, D., Loughland, R. and Aspinall, S. J. 1997. Habitat use by houbara bustard (*Chlamydotis undulata macqueenii*) in arid shrubland in the United Arab Emirates. - Journal of Arid Environments 35: 111-121.

Loxdale, H. D., Lushai, G. and Harvey, J. A. 2011. The evolutionary improbability of 'generalism' in nature, with special reference to insects. - Biological Journal of the Linnean Society 103: 1-18.

Mckinney, M. L. 1997. Extinction vulnerability and selectivity: Combining ecological and paleontological views. - Annual Review of Ecology and Systematics 28: 495-516.

Olson, D. M., Dinerstein, E. D., Wikramanaya, K. E., Burgess, N. D., Powell, G. V. N, Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P. & Kassem, K. R. 2001. Terrestrial ecoregions of the world: a new map of life on earth. - BioScience 51: 933-938.

Pianka, E. R., King, D. and King, R. A. (eds.). 2004. Varanoid lizzards of the world*,* Indiana University Press, Bloomington, Indiana.

Rachkovskaya, E. I. 1995. Vegetation map of Kazakhstan and Middle Asia (Desert region). Russian Academy of Sciences, Saint Petersburg.

Rajabov, T. 2009. Ecological assessment of spatio-temporal changes of vegetation in response to piosphere effects in semi arid rangelands of Uzbekistan. Land Restoration Training Programme, Reykjavik.

Riou, S. and Combreau, O. 2014. Male territories and the lek-like mating system of MacQueen's Bustard *Chlamydotis macqueenii*. - Journal of Ornithology 155: 959-967.

Steen, H., Yoccoz, N. G. and Ims, R. A. 1990. Predators and small rodent cycles - an analysis of a 79-year time-series of small rodent population fluctuations. - Oikos 59: 115-120.

Vinogradov, A. V. and Mamedov, E. D. 1975. Pervobytnyi Lyavlyakan: Etapy drevneishego zaseleniya i osvoeniya Kyzylkumov (In Russian) (Primitive Lyavlyakan: Periods of ancient settlement and new land development in Kyzylkum) Moscow, Nauka.

Wright, H. L., Lake, I. R. and Dolman, P. M. 2012. Agriculture—a key element for conservation in the developing world. - Conservation Letters 5: 11-19.

Yang, W. K., Qiao, J. F., Combreau, O., Gao, X. Y. and Zhong, W. Q. 2002. Display-sites selection by houbara bustard (*Chlamydotis undulata macqueenii*) in Mori, Xinjiang, People's Republic of China. - Journal of Arid Environments 51: 625-631.

Appendix 1 Photos of the main shrub assemblages of the southern Kyzylkum

Photos of the main six shrub assemblages of the southern Kyzylkum Desert, Uzbekistan, classified during this study. (Please note that each photo is an example of what we consider to be a typical representation of a given habitat type. Depending on an area, mean height of shrub sward and, to some extent, shrub species composition may vary within each habitat type due to variation in topography and soil within each shrub assemblage)

Artemisia

Salsola rigida

Salsola arbuscula


Astragalus

Calligonum


Saxaul

Appendix 2 Краткое содержание

Одним из путей сохранения видов, которым угрожает исчезновение, является выпуск разведенных в неволе особей в природу. Но, прежде чем принимать такие меры, необходимо исследовать потенциал механизмов которые могли бы использваться для поддержания продуктивности диких птиц с целью смягчения пресса, вызванного изъятием особей из популяции. Дрофа-красотка или джек (*Chlamydotis macqueenii*) занесена в список глобально-угрожаемых видов со статусом VU – угрожаемый. Ее численность в Центральной Азии продолжает снижаться, в основном в результате нерегулируемой охоты и отлова в период миграций и на местах зимовки.

Цель данной работы - изучить некоторые аспекты биологии мигрирующей популяции джека в период размножения, знание которых может быть необходимым для сохранения вида. Полевые работы проводились в весенний период 2012-2015 гг и включали в себя методы дистанционной выборки (distance sampling) на точках и на автомобильных маршрутах, мониторинг гнездования, спутниковое мечение и замеры параметров местообитания на территории площадью более 14500 км^2, расположенной в пустыне Кызылкум в Узбекистане. Вопреки ожиданиям, на территории исследований нами не было обнаружено ни свидетельств негативного влияния плотности скота на численность самцов джека, ни значительного влияния выпаса скота на растительность. Особенности местообитания, выбираемые самцами джека на уровне ландшафта, скорее всего позволяют максимально улучшить видимость их токования, что подтверждается более высокой плотностью самцов на более ровных участках ландшафта, с более низкой кустарниковой растительностью и бóльшим покрытием гравия. Впервые была сделана оценка плотности самцов на данной территории, основанная на стандартизированных учетах и стратификации по различным местообитаниям, а также дана общая оценка численности джека для региона. Не было обнаружено взаимосвязи между видовым составом кустарниковой растительности, плотностью скота и успешностью гнездования джека, но выживаемость гнезд, размещенных в более высокой растительности была выше. Мониторинг с помощью спутниковых передатчиков показал высокую привязанность самцов к их токовым участкам, а самок - к старым гнездовым территориям при повторном гнездовании. Было

также обнаружено, что в послегнездовой период взрослые птицы используют совершенно иные, более богатые растительностью районы, часто расположенные за пределами территорий, используемых в период размножения.

Все выше перечисленное дает основания предполагать, что джек отлично адаптирован к различным местообитаниям и может довольно успешно сосуществовать с умеренной пастбищной нагрузкой. В то же время, ничто не указывает на какие-либо конкретные меры по смягчению пресса, вызванного нерегулируемой охотой, путем поддержания естественной продуктивности дикой популяции, по-крайней мере в условиях пустыни Кызылкум и, возможно, по всему гнездовому ареалу вида в Центральной Азии. Это в свою очередь означает, что в близжайшее время наиболее подходящим решением вопроса сохранения вида, вероятнее всего, является использование ограниченных и устойчивых квот на добычу джека в послегнездовой период, основаных на аккуратных оценках демографии отдельных популяций (учитывающих продуктивность гнездования и выживаемость молодых и взрослых птиц) и осваиваемых только при обязательном и эффективном контроле на местах. В заключение, обсуждаются возможности применения ключевых результатов данного исследования для сохранения популяций джека в пустыне Кызылкум и предлагаются приоритеты для дальнейших исследований в данном направлении.