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Post-Soviet land-use change and conservation of avian biodiversity across the Eurasian steppe belt

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CHAPTER 1

Introduction

1. Background and state of research

1.1 The Eurasian steppes – a unique grassland ecosystem

The Eurasian (Pontian) steppes stretch from Ukraine to the Altai Mountains in Southern Siberia. They are characterised by a distinct latitudinal zonation: from north to south, belts of forest steppe, tall-grass steppe, short-grass steppe and desert steppe can be distinguished along a gradient of increasing aridity.

Once a vast ocean of grass, the 'Great Steppe' has gradually been cultivated for rain-fed cereal farming, and the traditional lifestyle of the Turkic nomad tribes travelling the grasslands with their horses, sheep and cattle has given way to more intensive livestock breeding systems. This process started early in Ukraine and the steppes of European Russia, where as early as the end of the 19th century hardly any steppe grassland remained in pristine condition. In contrast, arable farming started later in the area of today's state of Kazakhstan, and remained restricted to small pockets of fertile steppe near Cossack settlements until the collectivisation of the nomadic tribes under Josef Stalin in the 1930s. A major campaign to cultivate the steppes of Kazakhstan and Russian Western Siberia was launched in 1953 under Nikita Khrushchev (McCauley 1976), leading to cultivation of more than 35 million ha steppe (25 million ha in Kazakhstan alone) by 1960 and turning the eastern (Asian) steppes into the breadbasket of the Soviet Union. This 'Virgin Lands Campaign' transformed the face of the Eurasian steppes and led to large-scale changes in society and ecology.

Naturally, grasslands are particularly vulnerable to conversion into croplands, but large and contiguous expanses of near-natural grasslands have hitherto been preserved in the Eurasian steppes, with more than 10 % of the world's remaining grasslands situated in Kazakhstan (Loveland *et al.* 2000). The sheer scale of contiguous, near-natural grassland makes the steppes of Kalmykia, the Russian Lower Volga, Western Siberia and especially Kazakhstan a unique grassland ecosystem, which is home to a number of endemic species, many of them threatened. The carpets of flowering tulips that dot the steppe in late April are spectacular, and the plains of silver-shining feather grass setting seeds in May are probably the largest in the world. The remaining grasslands and some agricultural habitat harbour a number of biome-restricted and endemic animals, including the enigmatic Saiga antelope *Saiga tatarica*, Steppe Marmots *Marmota bobac* and the Critically Endangered Sociable Lapwing *Vanellus gregarius*, but their future seems uncertain in a world of growing food and energy demand.

1.2 The dissolution of the Soviet Union and agricultural change on the Eurasian steppes after 1991

When Mikhail Gorbachev introduced more governmental transparency and freedom of speech ('glasnost') and fundamentally restructured the political and economical system of the Soviet Union ('perestroika') in the mid-1980s, few would have predicted the magnitude and scale of change and turmoil that followed in society and economy of the former socialist states, reaching from Eastern Germany to the Pacific, with impacts on a global scale. During the past 20 years, everywhere in the former 'eastern bloc countries', the transition from state-controlled, planned to neoliberal, super-capitalist economies has led to pronounced changes in attitudes, production and consumption patterns.

In the states of the crumbling Soviet Union, the decade 1990 – 2000 was characterised by a breakdown of industry, infrastructure and social systems. Times of economic hardship caused massive waves of internal human migration and emigration mostly in the homeland of socialism, the former Soviet Union: people fled rural areas as state farms collapsed, and many, such as the ethnic German population of Siberia and Kazakhstan, moved back to their home countries.

Unsurprisingly, these changes had a profound impact on landscapes and biodiversity: rural areas now devoid of people reverted to wilderness, as widespread abandonment in the agricultural sector occurred across northern Eurasia. Systems of intensive livestock breeding collapsed as the animals were used as currency when wages were no longer paid out, or simply consumed as the shelves of food stores emptied.

The year 2000 marked a changing point – since then, in many (but not all) parts of the former Soviet Union, the economy has recovered strongly, the rural human population has started to increase again and industry and agriculture have recovered to a certain degree.

Nearly everywhere in the former Soviet Union, changes in land-use in the 1990s followed a trend that was subsequently reversed after 2000 alongside a recovery of the economy due to political stabilisation and growing exploitation of oil, gas and other resources. Although not restricted to it, land-use change was especially pronounced in the vast Eurasian steppes, stretching from Ukraine to the Altai Mountains in Russia.

Post-Soviet land-use change in the steppe zone was first described and quantified from satellite image analyses: De Beurs & Henebry (2004) and De Beurs *et al.* (2009) used a rather coarse, but large-scale analysis of NDVI trends in Kazakhstan and Russia to conclude that the changes in the observed land cover phenology between 1986 and 1999 were caused by large increases in abandoned land dominated by weedy plant species and reduced grazing pressure on pastureland. Finer-scaled satellite analyses combined with ground truthing conducted in the Kalmykian steppes in SW Russia suggested a pronounced decrease in the area of irrigated arable cultivation between 1989 and 1998, as well as a crash in livestock numbers and a recovery in vegetation communities formerly degraded due to high livestock densities (Hölzel *et al.* 2002).

These trends of abandonment and crashing animal numbers were supported by various publications at the end of the 1990s based on governmental statistics and land-use maps that became more freely available after the cold war ceased.

Evidence for large-scale declines in the area planted for crops (mainly wheat in the steppe zone) were first described by Meng *et al.* (2000), who evaluated an area of over five million ha abandoned wheat cultivation in Kazakhstan in 1998 (which later proved a more than twofold underestimate).

Suleimenov & Oram (2000) and Robinson & Milner-Gulland (2003) quantified the crash in domestic livestock numbers in Central Asia, with a more than 50 % decrease in Kazakhstan averaged for horses, cattle and sheep, and an overall decrease of 80 % in sheep. Spatial patterns in livestock reduction have been described (e.g. Lenk 2001, Kerven 2003), with some regions being less affected and others loosing virtually their entire domestic animal stocks. Seasonal livestock migration that had been restricted during the 20th century but still persisted, ceased in the 1990s, and the animals were concentrated year-round at pastures in the immediate vicinity of villages, leading to very imbalanced grazing patterns: vast areas of the steppes were completely ungrazed, while in the late 1990s overgrazing was evident around many villages (Robinson & Milner-Gulland 2003a, b, Kerven *et al.* 2006).

Although most evidence for these changes came from a few regions in Russia and Kazakhstan, recently published studies suggest that trends in arable farming and livestock breeding were similar across the Eurasian steppes (e.g. Charles 2010), probably with the exception of Ukraine, where livestock numbers crashed but agriculture was mainly abandoned in the mountainous areas in the west of the country rather than on the fertile steppe soils (Baumann *et al.* 2010).

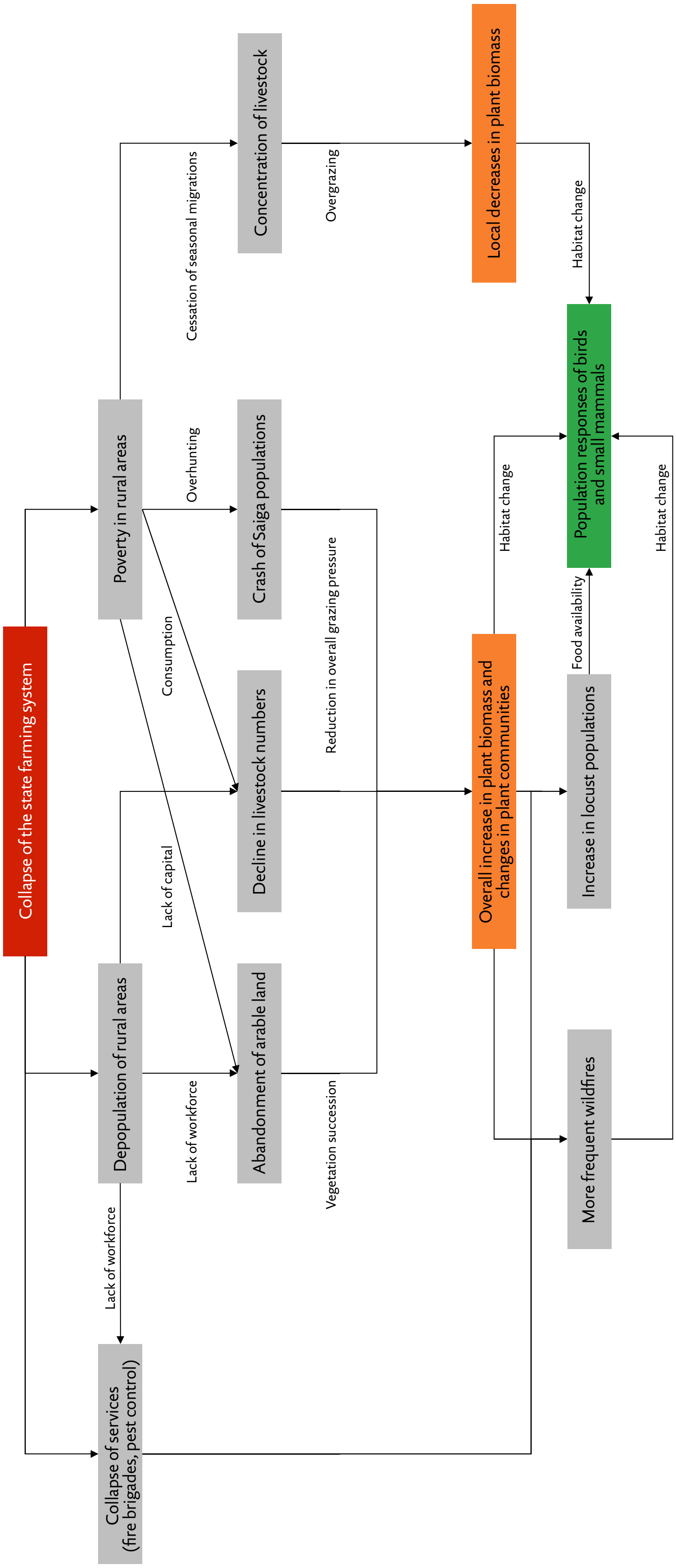

Figure 1. Cascade of landscape-scale changes in agricultural land-use following the collapse of the Soviet state farming system, and their impacts on habitats and biodiversity.

Human-induced changes caused carry-over effects on an ecosystem scale over huge areas (Figure 1). An interesting example is the increase of both number of and area burnt by wildfires in the steppe zone of the former Soviet Union. Dubinin *et al.* (2010) traced fires using satellite data and found a massive increase in steppe fire area in Kalmykia, SW Russia from almost none in 1985 to more than 20 % of their large study area burnt in 2006 and 2007. An increased fire frequency was related to land-use changes, as an increase became obvious 5 – 6 years after the collapse of livestock (mainly sheep) populations in Kalmykia, suggesting cessation of grazing during this period allowed biomass to accumulate and provide fuel for hot wildfires in many areas (Dubinin *et al.* 2010, 2011), a conclusion also supported by Hölzel *et al.* (2002). In Kazakhstan, the frequency and area of wildfires increased greatly in the same period as in Kalmykia (Khaidarov & Archipov 2001) and the reasons are likely to be similar. Fire is an important process in grassland ecosystems, as it results in changes in vegetation patterns and invertebrate numbers and thus shapes habitats and influences food availability for vertebrate species (e.g. Bendell 1974, Bock 1992, Rahmig *et al.* 2009).

1.3 Responses of animal biodiversity to land-use changes in the steppe zone

The impact of agricultural change on the biodiversity of the steppes of the former Soviet Union remains poorly studied and is mostly restricted to single-species assessments or anecdote observations.

Birds are among the best studied organisms in this regard. First evidence for effects of changing land-use was compiled for a number of birds of prey: Sanchez-Zapata *et al.* (2003) used road surveys in various habitats in eastern Kazakhstan to conclude that agricultural abandonment might have benefitted raptors that are sensitive to human disturbance. They speculated that a decrease in grazing pressure and subsequent vegetation succession might have rendered large steppe areas unsuitable for birds that need to detect their mammalian prey in open areas, such as the Vulnerable Lesser Kestrel *Falco naumanni* (Tella *et al.* 2004). Decreasing grazing pressure was also suggested to have led to declines in Caspian Plover *Charadrius asiaticus* populations in the Southwestern Russian steppes and in Kalmykia (Fedosov & Belik 2010). Agricultural abandonment on the Eurasian steppes has been linked to an increase in steppe bird populations utilising arable farmland: the complete recovery to pre-1950 levels of the much decimated eastern Little Bustard *Tetrax tetrax* population was attributed to agricultural change (Gauger 2007), as 30 % were found breeding on abandoned wheat fields in Russia in the late 1990s (Shlyakhtin *et al.* 2004), and Koshkin (2011) found a similar preference for abandoned fodder grass fields in a recent study in Kazakhstan. Oparin (2008) found evidence in a multi-species survey on the steppes of the Saratov region (Southern Russia) that abandonment of cereal cultivation boosted the numbers of larks, Siberian Stonechat *Saxicola maura* and Booted Warbler *Hippolais caligata*, and intensive grazing benefitted wheatears and the White-winged Lark *Melanocorypha leucoptera*. Recently, Fedosov (2010) suggested a massive increase in Calandra Lark *Melanocorypha calandra* populations in Kalmykia to be caused by decreased grazing pressure. Frequent breeding and high nesting success of Pallid Harrier *Circus macrourus* in abandoned wheat fields was described by Terraube *et al.* (2008). Impacts on other species groups, such as the steppe-typical small mammal communities, are likely to have been equally pronounced, although quantitative data are largely lacking and most publications are rather anecdotal.

A recovery in Russian Steppe Marmot *Marmota bobac* populations was linked soon after the collapse of the Soviet Union to abandonment of arable fields and human depopulation of rural areas resulting in decreasing hunting pressure (Bibikov 1991). Numbers have been increasing in Kazakhstan ever since, probably due to decreased hunting pressure and a recolonisation of abandoned fields (Nerger 2007). It seems likely that this had a positive effect of survival and productivity of large raptors such as Imperial or Steppe Eagles *Aquila heliaca* and *nipalensis*, which feed to a large extent on marmots and other small mammals.

Anecdotal evidence suggests that the increased grazing pressure around settlements and the resulting decrease in vegetation height and cover led to an explosion in the populations of certain souslik species, mostly *Spermophilus major* and *Citellus pygmaeus*. Especially around settlements in the short-grass steppe, several hundred to over a thousand sousliks can be observed synchronously from a single vantage point in July and August (own data 2006 – 2010), providing a rich food source for birds of prey. Concentrations of raptors at these overgrazed steppe swards can comprise up to 130 steppe eagles preying on *Spermophilus major* in August (J. Kamp own data, Torghay region 2009). Also, more complex interactions in grazed areas are likely, as sousliks create breeding habitat for burrow-nesting birds (such as Northern Wheatear *Oenanthe oenanthe* and Isabelline Wheatear *Oenanthe isabellinus* in the steppe zone) – indeed very similar to the three-way interaction between livestock, Plateau Pikas *Ochotona curzoniae* and burrow-nesting snowfinches described by Arthur *et al.* (2008) for the Tibetan Plateau.

Responses of insects to agricultural abandonment and changing grazing patterns are likely to have been equally pronounced, but published evidence is restricted to species considered as crop pests. In July 1999, billions of Italian Locusts *Calliptamus italicus* invaded Astana, the recently established new capital of Kazakhstan, and caused panic among the population and traffic accidents – a situation that had never occurred in Soviet times (Toleubaev *et al.* 2007). Several 'infestations' of this 'plague' were observed during the following two years and stimulated intensive research into the drivers of these mass breeding events (Wilps *et al.* 2002, IPP Consultants 2003, Toleubaev *et al.* 2007). It became clear very soon that populations were boosted by a greater availability of suitable soil conditions and palatable, nutrient-rich biomass found on abandoned fields compared to virgin steppe, and local overgrazing contributed to this: estimates by the Soviet pest control system suggest an absence of Italian Locusts on used arable fields, a mean August density of 3.5 Ind. / m^2 in virgin, moderately grazed steppes, but a staggering 20 – 26 Ind. / m^2 on fallow and abandoned fields of various age and similarly high numbers of 20 Ind. / m^2 on overgrazed steppe swards in the vicinity of settlements (Toleubaev *et al.* 2007).

It seems likely that the increased availability of locusts, and thus the unlimited provision of food especially late in the breeding period increased survival, breeding success and population size in many insectivorous birds, although quantitative studies are lacking.

The collapse of the Soviet economy resulted in widespread poverty, especially in rural areas where the human population was dependent on large state farms. The strongest drivers behind trends in wild animal populations were probably the changes in habitat described above; however, direct implications resulting from deteriorating living standards became obvious soon after the dissolution of the state farms in 1994. A particularly well-researched example is the fate of the Saiga antelope *Saiga tatarica*, a large grazer that once roamed the steppes and semi-deserts of Eurasia in million-strong herds. With Kulan *Equus hemionus* and Goitered Gazelle *Gazella subgutturosa* hunted to near extinction early, Saigas were the only wild ungulates left in significant numbers grazing in Russia and Kazakhstan in the second half of the 20^{th} century. Valued as a source of meat, they were managed more or less sustainably in Soviet times, with hunting bans introduced when numbers were significantly reduced to allow population recovery (Bekenov 1998). Just as in domestic livestock, Saiga antelope numbers crashed in 1994 and subsequent years, when unemployment resulted in widespread poverty in rural areas after the closure of the state farms, as Saiga were poached heavily as an easy source of meat mostly by impoverished villagers (Kühl *et al.* 2009). Numbers were reduced from more than a million head in 1993 to a mere 30 000 by the year 2003 (Milner-Gulland *et al.* 2001, Robinson & Milner-Gulland 2003b) – a population decline of 97 % over a 10 year period. Additional pressure was put on the Saiga population by the fact that males were selectively hunted for their horns (which were, and still are, smuggled to China for traditional medicine), resulting in skewed sex ratios and reduced female fecundity which in turn accelerated the decline (Milner-Gulland *et al.* 2006). Saiga numbers have stayed low until recently, but are now showing signs of recovery, which has been attributed to more rigorous enforcement of anti-poaching legislation and the designation of new protected areas in Kalmykia and Kazakhstan (Singh & Milner-Gulland 2011).

Saiga and other large grazers are regarded as keystone species in the steppe and semi-desert ecosystems, and a landscape-scale impact of their grazing behaviour on vegetation, birds and other biodiversity seems likely, but studies quantifying this effect are sparse or anecdotal. For example, Bibikov (1991) still assumed that steppes not grazed by domestic livestock or wild ungulates are not colonisable by steppe marmots, but marmot numbers have been increasing strongly since the collapse of the Soviet Union even in areas without any livestock or grazers (Nerger 2007).

2. Study areas

The research presented here was conducted in three study areas in northern and central Kazakhstan (Figure 2). The largest part of the data analysed in chapters 2 – 5 was collected in an extensive area of pristine steppe and (partly abandoned) farmland in the Tengiz-Korgalzhyn region, Akmola district. Transferability of habitat models for Sociable Lapwing developed in Korgalzhyn region was tested on the cultivated and pristine steppes surrounding the vast Lower Irtysh river valley, Western Siberia (Pavlodar district). The data for the analysis of bird responses to grazing intensity (chapter 3) was gathered on the dry steppes and semi-deserts of the Torghay region, southern Kostanai district (Central Kazakhstan).

The study area in the Tengiz-Korgalzhyn region covers an area of approximately 13 500 km² and stretches between 49°48′ – 51°00′ N and 69° 32′ – 70°54′ E. It is situated in the south of the dry steppe-ecoregion, also termed short-grass steppe (WWF ecoregion 'Kazakh steppe', Olson *et al.* 2001). The area is dominated by the large saline, undrained Lake Tengiz (ca. 1 300 km²) fed by three steppe rivers and surrounded by numerous salt and freshwater lakes of various size (Schielzeth *et al.* 2008, 2010).

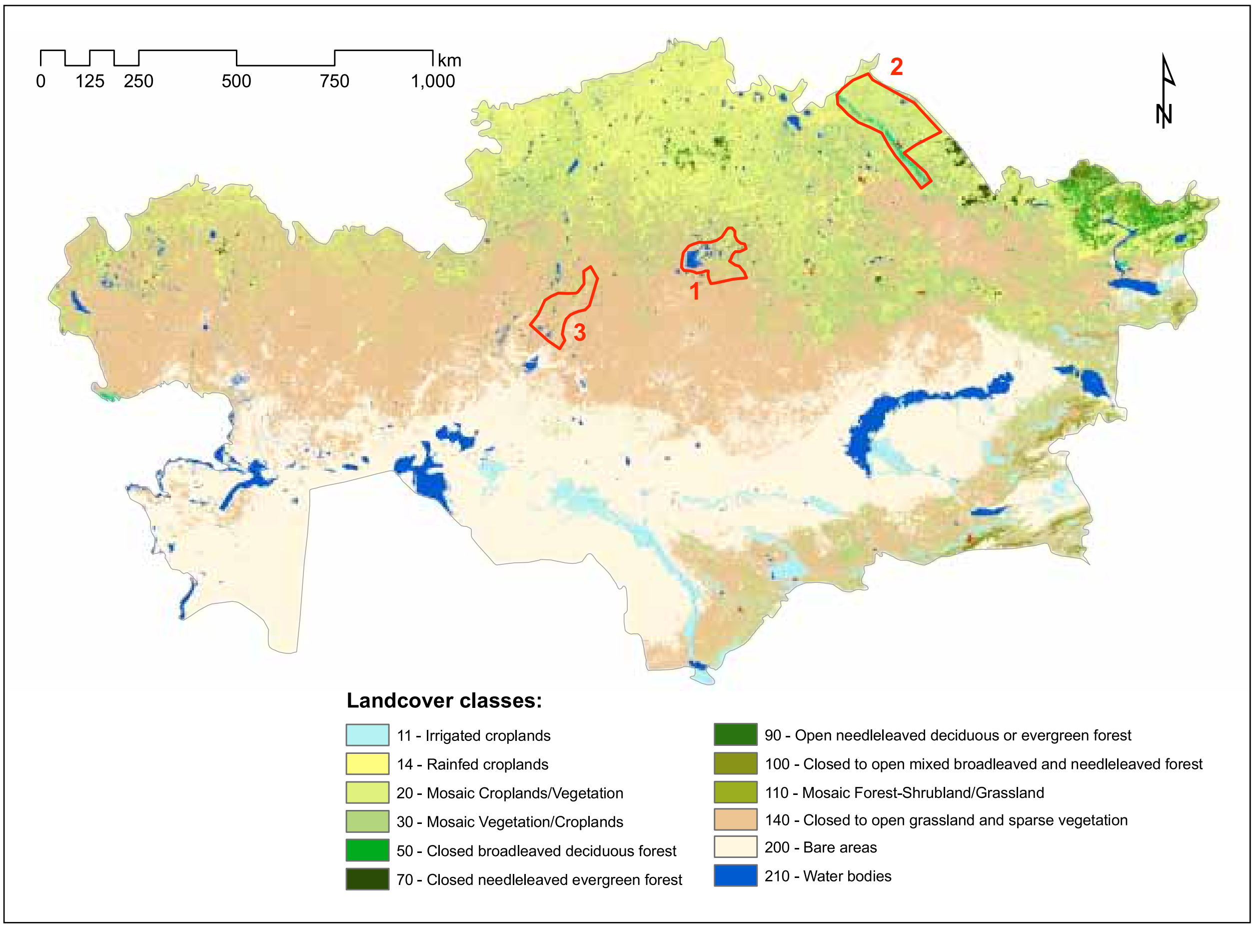

Figure 2. Location of the three study areas within Kazakhstan. (1 – Tengiz–Korgalzhyn, 2 – Lower Irtysh, 3 – Torghay.) Land cover classes are slightly modified after GlobCover 2009 (European Space Agency 2010).

The climate is extremely continental with an annual temperature amplitude of 80 K and with an annual mean temperature of 2.8 °C, a mean precipitation year total of 267 mm and a pronounced precipitation peak in summer (Korgalzhyn weather station, means 1975 – 1998, after Dieterich 2000)(Figure 3). In the north of the study area, soils are dominated by humus-rich Dark Kastanozems (Prasolova & Gerasimov 1955) that were cultivated nearly entirely where solonisation or high carbonate contents did not prohibit it. The southern part is characterized by shallower Light Kastanozems with thinner humus layers, used traditionally for grazing and often solonised (Prasolova & Gerasimov 1955). Solonchaks and solonets soils are distributed patchily throughout the area, and Meadow Soils are found in the river valleys (Prasolova & Gerasimov 1955).

The zonal vegetation of the short-grass steppe is dominated by Fescue *Festuca sulcata* and Feather grasses (mostly *Stipa lessingiana* and *S. capillata*), with stony areas, solonets soils and solonchaks hosting communities with a high diversity in Chenopodiaceae and numerous *Artemisia* species (Karamysheva & Rachkovskaya 1973). River valleys are fringed by extensive Willow *Salix spp.* thickets. Blossoming carpets of geophytes such as tulips (mainly *Tulipa schrenkii* and *T. patens*) are found after snow melt in spring in pristine steppe that had never been ploughed (Karamysheva & Rachkovskaya 1973, Sidorova 1988)

Plant communities of secondary succession on abandoned farmland vary with age, young abandoned fields and fallows often appear like rape *Brassica napus* fields due to a dominance of Cruciferaceae. After a few years weedy *Artemisia* species (e.g. *A. abrotanum, A. dracunculus*) cover vast expanses and create a more 'shrubby' appearance, whereas the oldest abandoned fields (at ca. 16 years age) show significantly higher cover of the native steppe grasses. Abandoned fields on saline soils with high carbonate content can be covered by species-poor communities of *Stipa spp.* and *Leymus ramosus* a few years after abandonment (Marinych *et al.* 2002). Many fields were planted with Crested Ryegrass *Agropyron pectinatum* to provide winter fodder for cattle in Soviet times, but most have not been resown for 10 – 15 years and gradually restore to steppe communities.

Overgrazed areas show low grass cover or lack grasses altogether, except Fescue that profits from non-intensive grazing. In the steppe zone, bitter and unpalatable *Artemisia* species and ruderals (many Chenopodiacae) remain instead as they are avoided by grazing livestock (Yunusbaev *et al.* 2003).

The Lower Irtysh study area in NE Kazakhstan stretches along the lower Irtysh river between the settlement Akku (= Lebyazhe, ca. 51°28'N / 77°46'E) and the Russian border at ca. 53°47'N / 75°03'E. Surveys covered an area of approximately 12 000 km². Away from the wide river floodplain (up to 16 km of inundated hay meadows, sedge mires and old-growth Willow / Poplar gallery forests), the south of the area is characterised by dry feathergrass (*Stipa spp.*) steppes, but the north situated in the forest steppe dominated by tall grasses, herb-rich steppe communities and insular birch (*Betula pendula*) forests (WWF ecoregions 'Kazakh steppe' and 'Kazakh forest steppe', Olson *et al.* 2001).

The climate is similar to the Korgalzhyn study area, but even more continental with colder winters (minimum January temperatures of – 52 °C) that last longer. Annual mean temperature at the weather station Pavlodar is 3.1 °C, the annual mean precipitation total amounts to 318 mm (Hayashi *et al.* 2006) (Figure 3).

Soil geography varies in the study area with Southern Chernozems, Meadow Chernozems and Solonets soils in the north, and Dark Kastanozems in the south, interspersed by solonchaks. Land-use patterns are similar to the Korgalzhyn study area, but a much larger proportion of the area was farmed during Soviet times. Climax states of steppe communities, rather tall and herb rich, are dominated by *Stipa capillata* and *Kochia siversiana* (Cheng & Nakamura

2007), whereas abandoned farmland shows similar associations as in the Korgalzhyn study area, with early stages dominated by *Artemisia absinthium*, and late stages restoring to steppe-like communities with *Stipa capillata*, *Artemisia austriaca*, *Medicago falcata*, *Kochia prostrata* and *Leymus ramosus* (Hayashi 2006, Cheng & Nakamura 2007).

The study area in the Torghay region covers an area of approximately 13 000 km² and stretches between 48°30′ – 50°21′ N and 63°08′ – 65°30′ E. It is situated in the desertified steppe and semi-desert belts (WWF ecoregion 'Kazakh semi-desert', Olson *et al.* 2001).

The climate is continental, but drier and slightly warmer than in the other two study areas: the mean annual temperature at Torghay meteorological station is 4.8 °C, the mean annual precipitation total 221 mm with no obvious peaks in precipitation (Walther *et al.* (1975), updated with data from http://rp5.kz, cf. Figure 3). Soils are similar to those in the Korgalzhyn study area, but overall, Light Kastanozems with shallow humus layers prevail, and nearly all soils are rather saline. This renders them unsuitable for agriculture, leading to a near-exclusive use as pastures in Soviet times.

In the north of the region, dry steppe plant communities are widespread, similar to those in the Korgalzhyn region dominated by Feather Grasses and Fescue. Towards the south, they are gradually replaced by semi-desert communities with fewer grasses and a dominance of *Artemisia* species even in ungrazed areas and many Chenopodiaceae, whereas *Stipa* is restricted to the hillslopes.

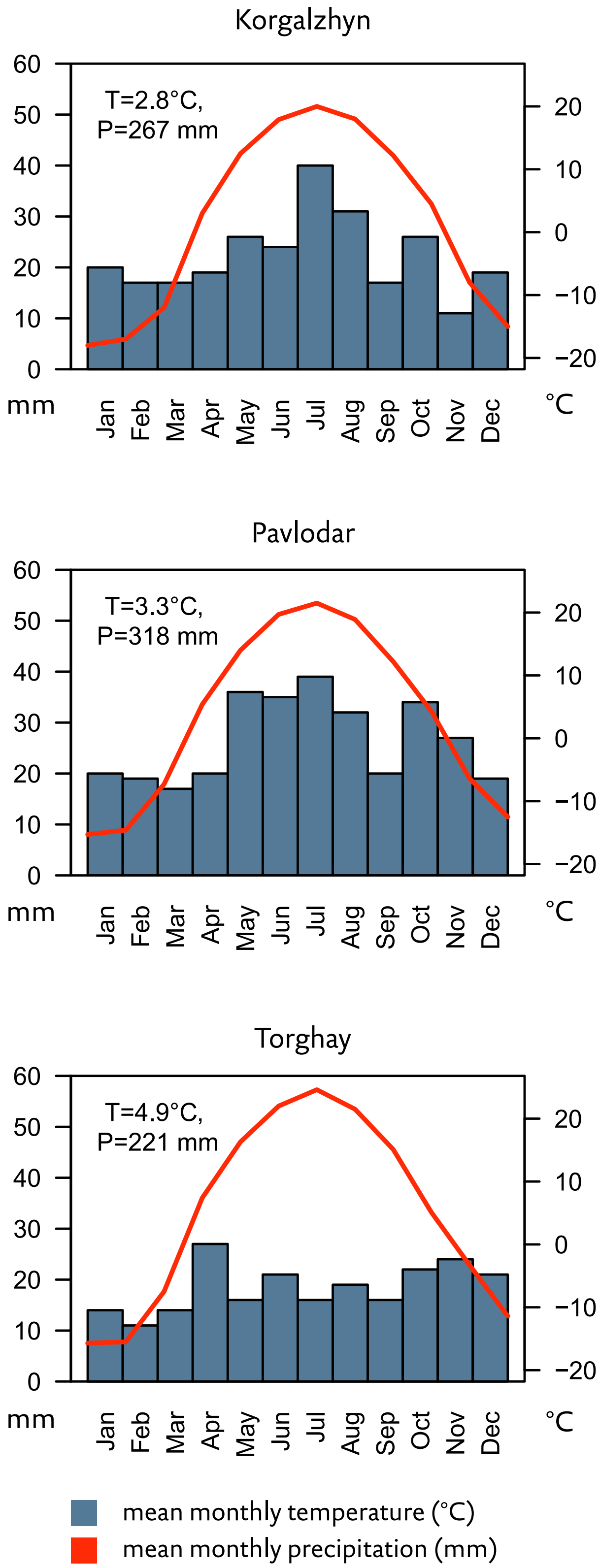

Figure 3. Monthly means of precipitation (bars) and temperature (lines) for the three study areas (weather stations Korgalzhyn, Pavlodar, Torghay) over an observation period of at least 25 years.

3. Background and aims of the study

Although land-use change on the steppes of the former Soviet Union between 1991 and 2000 is well documented in the literature and its impact on biodiversity has been studied locally, trends in land-use since the year 2000 have not yet been analysed. The impact on biodiversity of agricultural changes is poorly understood for the entire period since 1991.

Grassland birds have been declining more than other species in North and South America, South America and Europe, and have been identified as a group of high conservation concern by BirdLife International.

The overall goal of this PhD-study was thus to improve knowledge on population ecology, habitat use, population status and threats of a suite of characteristic grassland birds of the Eurasian steppes, ultimately aiming at a utilisation of this information to inform decisions of conservation managers and influence future land-use policy.

In detail, the main aims of the research presented here were:

i) To provide a synthesis of agricultural land-use change on the Eurasian steppes for the past 20 years since the dissolution of the Soviet Union and predict future change.

ii) To evaluate the impacts of the described changes on a number of endemic and often threatened grassland bird species, known as good indicators for change in overall biodiversity.

iii) To use these data to predict possible future responses of steppe birds to land-use change and identify vulnerable species.

iv) To provide previously unavailable baseline population density estimates for steppe birds.

v) To make information on population sizes and likely threats available for future reassessments of the Red List status of data deficient steppe birds.

vi) To examine population status and habitat requirements of two threatened steppe birds in order to more effectively plan conservation measures on the ground.

4. Structure of the thesis

This thesis consists of four scientific articles examining the impact of agricultural land-use change following the break-up of the Soviet Union in 1991 on a characteristic suite of steppe birds in Eurasia. Three papers have been published in peer-reviewed, ISI-ranked journals; one has been submitted but not yet accepted.

The first paper (chapter 2) contains an evaluation of general post-Soviet agricultural land-use change in the steppe zone of Kazakhstan and presents modelled densities (using a Distance Sampling approach) for a suite of steppe birds across different habitat and land-use types. Ultimately, future population changes in these species are predicted by relating bird population densities to forecasted change, as evaluated by socio-economic interviews with land managers. This allows vulnerable species to be identified and prioritised for conservation measures where appropriate.

The remaining chapters evaluate fine-scale mechanisms behind responses of key species and species groups to varying intensity in agricultural use of their habitats using statistical habitat modelling approaches:

In chapter 3, responses of five lark species, the most abundant steppe birds in Eurasia, towards the intensity of domestic livestock grazing and arable abandonment are identified, and realised niches of this important steppe bird community modelled using flexible regression approaches and a machine learning technique. Population changes since the break-up of the Soviet Union are reconstructed based on known habitat changes.

In chapter 4, the habitat selection of a critically endangered wader (shorebird) endemic to the steppes of Kazakhstan and fringing regions of Russia, the Sociable Lapwing *Vanellus gregarius*, is modelled on two different scales in order to develop hypotheses for a massive population decline during the Soviet and post-Soviet era and suggest conservation measures. Nest site selection is related to grazing pressure of domestic ungulates in order to determine possible responses to changing grazing patterns post-1991.

In chapter 5, an assessment of the population status of the red-listed Black-winged Pratincole *Glareola nordmanni* is presented, combining a new world population estimate based on surveys across the breeding range, fine-scale habitat modelling and a breeding ecology study. Conservation needs are identified and a reassessment of the current IUCN red list status of the species is suggested.

Chapter 6 gives a general synthesis of the study results, puts the most important conclusions into context and suggests possible future research options.

CHAPTER 2

Kamp J, Urazaliev R, Donald PF, Hölzel, N (2011)

Post-Soviet agricultural change predicts future declines after recent recovery in Eurasian steppe bird populations

Biological Conservation 144: 2607 – 2614

Author contributions: JK collected the data, conducted the analysis and wrote the paper.
RU assisted with socio-economic interviews in Kazakh language and logistics.
PFD and NH gave advice on sampling design, data analysis and write-up.

Summary

The socioeconomic impacts of the break-up of the Soviet Union after 1991 have resulted in massive changes in agriculture on the Eurasian (Pontian) steppe, most of which is now confined to Kazakhstan. Recent trends in agriculture are well documented but their impacts on the characteristic bird community of this vast region, which contains over 10 % of the world's remaining grasslands, are poorly understood. We modelled bird population density in a representative region in central Kazakhstan along a land-use gradient ranging from pristine steppe to arable fields and heavily grazed pastures. Long-abandoned arable fields and ungrazed pristine steppe were the most important habitats for most species, and post-1991 abandonment of arable agriculture suggests that many species have enjoyed a period of significant population growth. Livestock concentration effects, leading to high grazing pressure in small areas, are also likely to have benefitted several species of high conservation concern. However, analysis of land-use statistics and socioeconomic surveys among land managers suggest that recent and predicted future trends in agriculture in the steppe zone, particularly the reclamation of abandoned cereal fields and reduced grazing pressure, may cause populations of most species, including a number of biome-restricted species, to decline in the near future. We discuss possible conservation solutions, including improvements in the protected area system and land-sparing options.

1. Introduction

The expansion and intensification of agriculture have been major causes of global biodiversity loss and species endangerment in recent decades (Green *et al.* 2005, Tilman 1999). World food demand is predicted to double by 2050 (Tilman *et al.* 2002), and the increasing cultivation of bioenergy crops will place additional pressure on natural habitats (Field *et al.* 2008). Grasslands are especially vulnerable to conversion into croplands, and with only 5 % of their total area covered by protected areas (Brooks *et al.* 2004) they are the least protected habitat worldwide.

Grassland birds have been declining more than other species in North and South America (Birdlife International 2010a, With *et al.* 2008) and Europe (Chamberlain & Fuller 1999), and have been identified as a group of high conservation concern by BirdLife International.

The Eurasian (Pontian) steppes (Figure 1) have largely been neglected by conservation research so far despite comprising 11 % of the world's remaining natural grasslands (Loveland *et al.* 2000). The 'Great Steppe', situated entirely within the borders of the former Soviet Union, harbours a number of biome-restricted species, several of which have declined over the last decades and are included in the International IUCN Red List (BirdLife International 2010b). Equally important, the Eurasian steppes are home to large and healthy populations of 'farmland birds' (such as Skylark *Alauda arvensis* and Yellow Wagtail *Motacilla flava*) which are declining significantly as a group across Western and Central Europe (Donald *et al.* 2006, Vorisek *et al.* 2010).

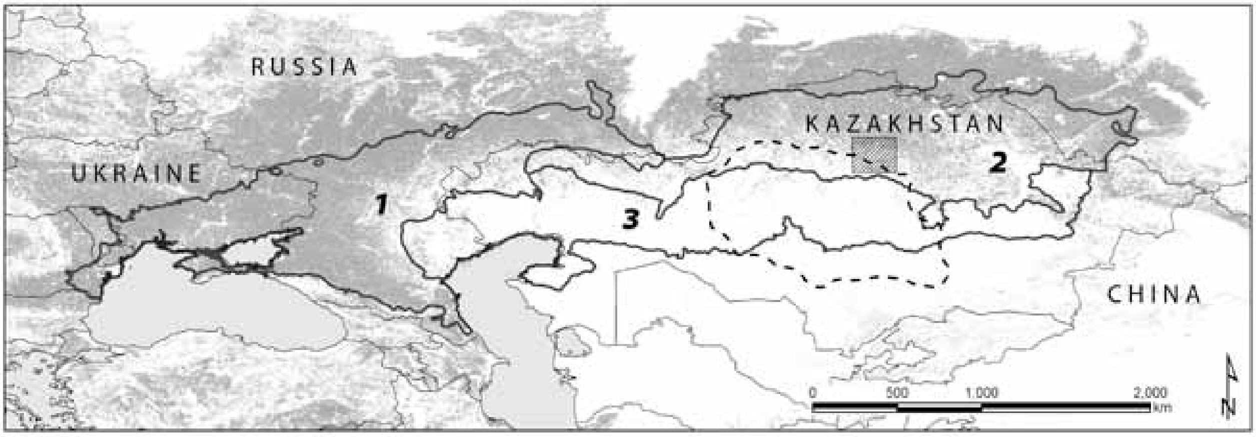

Figure 1. Steppe ecoregions in Eastern Europe and Central Asia: 1 – Pontic steppe, 2 – Kazakh steppe, 3 – Caspian and Kazakh desert steppes and semi-deserts (modified after Olson *et al.* 2001). Pontic and Kazakh steppe are often lumped and treated as 'Eurasian' or 'Pontian' steppe. Shaded grey areas are dominated by (partly abandoned) arable agriculture (landcover classes 'rainfed croplands' and 'mosaic croplands / vegetation', GlobCover 2009 (European Space Agency 2010)). The hatched box gives the location of our study area, the dashed line delineates the territory of the 'Altyn Dala Conservation Initiative'.

Within the Eurasian steppe belt, huge areas of steppe have been cultivated during the last 250 years, especially in Ukraine and Russia. In Kazakhstan, large-scale cultivation started comparatively late, when about 25 million ha were ploughed between 1954 and 1960 during the 'Virgin Lands Campaign' (McCauley 1976). The massive changes in economy and society following the dissolution of the Soviet Union in 1991 and the subsequent transition from a planned to a market economy had a severe impact on the state-controlled agricultural system. During the 1990s, this led to massive declines in livestock and wild ungulate numbers (Robinson & Milner-Gulland 2003), changes in grazing patterns (Kerven *et al.* 2006, Robinson *et al.* 2003) and the abandonment of vast areas of arable land (De Beurs & Henebry 2004, Hölzel *et al.* 2002) in the steppe zone. It is likely that these processes affected biodiversity at a large scale. However, there have been surprisingly few attempts to quantify the responses of biodiversity to these changes, or the potential for restoration of abandoned land to steppe.

Since around 2000, many of the post-Soviet trends in agriculture were reversed, with expansion and intensification of agriculture in the steppe zone of Kazakhstan and new increases in livestock numbers. Habitat alteration and loss due to expanding and intensifying agriculture and to overgrazing have been considered causes of recent declines in a number of threatened steppe bird species (e.g. Antonchikov 2005), but quantitative assessments are lacking.

We quantified large-scale densities of steppe bird species in relation to land-use for the first time and relate these to post-Soviet and predicted future trends in agriculture. This allowed us to explain current distribution patterns in the steppe bird community, to predict population responses to likely future land-use changes over vast areas of central Eurasia, and to suggest possible conservation intervention options.

2. Methods

2.1 Study region

The study area covered the Korgalzhyn region (9300 km²) of Akmola district in Central Kazakhstan (Figure 1). It is situated in the southern wheat belt of Kazakhstan, south of approximately 51°30′ N (McCauley 1976), which was the area most affected by agricultural change after 1991 (Dieterich 2000). Korgalzhyn, the administrative centre is situated at 50°35′ N, 70°00′ E. The main vegetation communities are dominated by the feather grasses *Stipa lessingiana* and *Stipa capillata*, the native fescue *Festuca sulcata* and wormwoods *Artemisia*. Precipitation varies strongly between years. With 254 mm, the annual total for 2009 was slightly below the 1970 – 2010 average of 267 mm (Korgalzhyn weather station *in litt.*). Approximately 42 % of the region's terrestrial area was cultivated for arable farming in Soviet times (1959 – 1991), but 68 % of farmland were abandoned by 2002, since when reclamation started. The southern parts of the region were traditionally used as pastures by nomadic tribes, but seasonal migration routes were shortened in Soviet times. Since independence, livestock has been concentrated around human settlements, leading to local overgrazing (sensu Wilson & MacLeod 1991), with huge areas of steppe remaining ungrazed.

2.2 Study design

We surveyed birds in the six dominant land-use and habitat categories in the region, namely

i) arable fields in cultivation,

ii) recently (1 – 4 years) abandoned arable fields,

iii) long (5 – 18 years) abandoned arable fields,

iv) fodder grass fields (cut for hay in July / August, with crested wheatgrass *Agropyron cristatum*)

v) heavily grazed to overgrazed steppe (mean vegetation height 9.6 cm ± 1.7 standard error (SE), n = 90 plots) and

vi) ungrazed ('pristine') steppe (mean vegetation height 27.4 cm ± 1.5 SE, n = 252 plots).

Fallows were included in the category 'recently abandoned fields' as it was often difficult to decide if they were deliberately left fallow or recently abandoned. These six land cover categories between them covered almost the entire terrestrial area of the study region and are representative of such habitats across much of the Eurasian steppes.

Arable habitats were surveyed on the territory of four former Soviet state farms with different levels of abandonment: high on 'Druzhba' farm (916 km², 88.1 % of former cereal cultivation abandoned and 100 % of fodder grass fields not re-sown since 1995), intermediate on 'Arykty' (589 km², 50.7 % / 89.1 %) and 'Kurgald'zhinskii' farms (650 km², 62.2 % / 79.7 %) and very low on 'Lenin' farm (554 km², 12.5 % / 57.1 %).

Since the mid-1990s, domestic livestock grazing has been concentrated within a 10-km radius around settlements (Kamp *et al.* 2009b). The cattle and sheep of every household are collected by shepherds in the early morning, driven radially out of the villages in herds and brought back every evening. For surveys, the two largest areas of contiguous grazed steppe (7 000 and 2 200 ha) were selected around the town of Korgalzhyn and the village of Aktubek. Steppe areas that had never been ploughed and where pastoralism ceased in the mid-1990s were classified as 'ungrazed'. Since no such habitats were available within the state farms, we selected an area of steppe about 60 km SW of Korgalzhyn (and at 639 km² of similar size to the state farms), where no grazing had occurred since 1996. This area was situated at the same latitude of the southernmost former state farm covered and comprises the same vegetation communities formerly found in the arable areas (Burlibaev *et al.* 2007).

2.3 Bird surveys

We counted all birds present along 171 line transects of 500 m length, distributed across all six land-use categories (Table 1), using a regular sampling design.

On each of the state farms, a block of 30 – 35 fields was selected around a random start point, except on Kurgald'zhinskii farm, where only 16 fields were included in the block. In the ungrazed steppe area, three blocks of 10 × 5 km were selected at random. Within these blocks, transects were walked every 2 km, the starting point being always situated 1 km away from the field corner at the centre of the field edge. Mean field size was 410 ha ± 126.8 SD (range 130 – 766 ha), with no delineating structures such as fences or hedge rows. In the heavily grazed areas around villages, transects were walked every 0.5 km, along three routes, each commencing at the village edge and extending radially for 5 km.

Transects were walked between 5 May and 23 May 2009. In order to adequately record long-distance migrants, some of which arrive as late as mid-May (Table 1), we repeated each count between 25 May and 13 June 2009. Surveys were conducted from dawn until 10 am, after which bird activity declined markedly. Distance sampling was used to account for varying detectability between habitats and species (Buckland *et al.* 2001). We estimated the perpendicular distance to each bird sighted (excluding flyovers) along the transect within distance bands of 0 – 5 m, 5 –10 m, 10 – 25 m, 25 – 50 m, 50 – 100 m, 100 – 200 m and 200 – 500 m. Laser range finders (Bushnell Scout 1000) were used to calibrate distance estimation.

Species that occurred in low densities such as raptors and cranes were counted along 41 car transects with a total length of 840 km (mean 21.6 km ± 3.3 SE), placed opportunistically along roads and driveable tracks in all study sites and land-use categories. The position of the transects was predetermined by the routes used to travel both within and between the sample blocks. While driving at low speed (20 – 40 km / h), we recorded the approximate distance and angle to all individuals observed. Apart from the driver, there was always one further observer in the car focusing on detection of birds. All data used for density estimation were collected on dirt tracks that had little effect on surrounding habitat, no parallel-running electricity poles and traffic rates <10 cars / day, between 05 May and 30 June 2009.

Densities of colonial species cannot be estimated reliably using Distance Sampling. Thus, in May and June 2009 we conducted additional, targeted surveys for two key steppe species, Black-winged Pratincole *Glareola nordmanni* and Sociable Lapwing *Vanellus gregarius*. The distribution of both species has been studied in the area since 2004 (Kamp *et al.* 2009a, b). All colony sites occupied at least once since 2006 were visited between 1 May and 15 June and the number of birds counted recorded. Where colonies were visited more than once, the maximum number of birds present was used for further analysis.

Additionally, we regularly stopped at vantage points while travelling within and between our sample blocks and surveyed the area using a telescope, but also watched out for pratincoles and lapwings during the walked and driven transects. Finally, non-random car transects with a total length of approximately 600 km were conducted in search of pratincole colonies.

By combining the three count methods, we were able to model densities for all land-use categories for 15 grassland bird species. For another 15 species recorded on the walked transects we were unable to gather enough registrations to derive robust estimates. These were mostly species not dependent on grasslands or scarce breeders in the study area (cf. Appendix 1).

2.4 Land-use statistics

Statistics on land-use were obtained from statistics agencies at three administrative levels. For the Republic of Kazakhstan, all figures were downloaded from the governmental statistics agencies' homepage (http://www.stat.kz). At district and regional levels, customised data were requested. For Akmola district, some newer figures were downloadable from http://www.akmola.stat.kz.

2.5 Socioeconomic surveys

We interviewed key stakeholders in agriculture and livestock breeding in our study area in an attempt to predict possible future trends in land-use and confirm recent trends as suggested by the land-use statistics.

A quantitative, structured questionnaire survey was conducted among the directors of 32 cereal-farming businesses spread evenly over the entire region. We were able to reach 24 small-scale farming enterprises (50 – 2000 ha farm size) and eight large agricultural companies (2000 – 18 000 ha farm size), representing 53 % of the 60 farming businesses registered in Korgalzhyn region in 2010. All interviewees were approached in person on their farmland during harvest to maximise response rates.

Additionally, a quantitative telephone survey was directed at private households involved in subsistence or commercial livestock husbandry. We used a random sample of all households connected to the landline network in Korgalzhyn region, equally stratified by settlement (n = 170 households in five settlements).

Semi-structured interviews (Bernard 2006) were conducted with key decision makers in the region's political administration and livestock owners (n = 13). All interviews were conducted by the first and second author, in Russian or Kazakh respectively, between 24 August and 30 September 2010.

2.6 Data analysis

For each transect, species richness (S) and the Shannon-Wiener Index of species diversity (H') were calculated. We tested for differences in species richness and diversity between land-use categories using Kruskal-Wallis non-parametric ANOVA, and compared the means between land-use categories by pairwise Mann-Whitney-U Tests with Bonferroni-corrected p-values (function `pairwise.wilcox.test` in R 2.12.1). Population densities were modelled for each bird species separately and numbers were corrected for detection probability in program DISTANCE 6.0 (Thomas *et al.* 2010). We assessed a number of detection models (uniform, half-normal and hazard-rate shapes) and selected the best-performing ones using Akaike's Information Criterion (AIC). As bird detections were assigned to a relatively small number of distance categories, we did not employ series expansions to avoid overfitting (Stanbury & Gregory 2009). Confidence intervals were bootstrapped with 999 iterations. In Distance Sampling analysis, only species with at least 60 detections and a coefficient of variation (CV) higher than 25 % were considered (Buckland *et al.* 2001). For early-breeding and resident species, detections gathered during the first count were used, while for late-arriving migrants, we used only detections made during the second count.

Car transects were treated as strip transects and observations were truncated at a distance of 200 m on both sides of the road, as there was evidence from walked transects that detection probability did not decrease strongly within this distance for larger species (e.g. still 80 % at 200 m for Pallid Harrier *Circus macrourus*). For the two colonial species, we divided the maximum number of birds counted by the total area of the relevant land-use type as derived from GIS land-use maps, separately for sub-units of grazed or ploughed land that were surveyed.

As habitat patches were extremely large and uniform (cf. 2.2) and most were flat or at most gently undulating, we did not expect strong landscape effects on density and distribution of most bird species.

In an attempt to assess possible future bird population trends in relation to habitat change, we predicted population size in 2020 relative to 2009 population size in the Korgalzhyn region. Differences in current and future population size were calculated and expressed as per cent change during the overall period.

The population size in 2009 was estimated for each species separately by multiplying mean, minimum and maximum (as given by bootstrapped 95 % confidence limits) bird density per land-use type with the area of every land-use type separately, and subsequently summed. Population size in 2020 was estimated by multiplying bird density per land-use type by the predicted area of each land-use type in 2020. This was predicted in a number of ways. First, farmers were asked during questionnaire surveys whether they were planning to reclaim land for cereals and fodder grass within the next 10 years and if so, how much. The area given by each farmer was summed to a total area for cereal and seed grass separately, and multiplied by 1.89 (as only 53 % of all farmers could be reached), with the assumption that our sample was representative. The area of cereals and fodder grass was then subtracted from the total area of abandoned farmland, as our interview results suggested that abandoned land would be reclaimed completely before new areas of pristine steppe would be ploughed. Interviews with decision makers in the agricultural department revealed a quantitative target for stock reduction on village pastures of about one third by 2020 to reduce overgrazing, and support for stock transfer to remoter pastures. As there is good evidence for a linear relationship between animal load and vegetation height in our study area (Kamp *et al.* 2009b), we projected overgrazed sward area to decline by 33 %. This area was then added to the area of habitat type 'ungrazed steppe', as no ploughing is currently permitted within 10 km of settlements (Korgal-zhyn Agricultural Dpt., pers. comm.). Redistribution of stock to areas currently classified as 'ungrazed' was assumed not to influence bird communities strongly, as no concentration effects are to be expected (Kerven *et al.* 2006) and stock density would be very low due to the vast areas available.

3. Results

3.1 Past and current trends in agriculture

Arable farming in the Kazakh Soviet Socialist Republic remained relatively unproductive until 1953, the start of the Soviet 'Virgin Lands Campaign'. A peak in the steppe area ploughed was reached in the late 1980s, followed by a massive decline since the collapse of the Soviet Union in 1991 (Figure 2A). In independent Kazakhstan, the area of cereals and fodder crops halved between 1991 and 1999, leaving approximately 12 million ha of cereal fields abandoned by the year 2000 (Figure 2B). Since then, cereal fields have been reclaimed and the area ploughed has increased again (Figure 2A and B). The area of fodder crops remains low compared to Soviet times (Figure 2B). Livestock numbers collapsed between 1993 and 1997, but then increased (Figure 2C). In our study region, a sharp increase was apparent in the period 2000 – 2009 (Figure 2D).

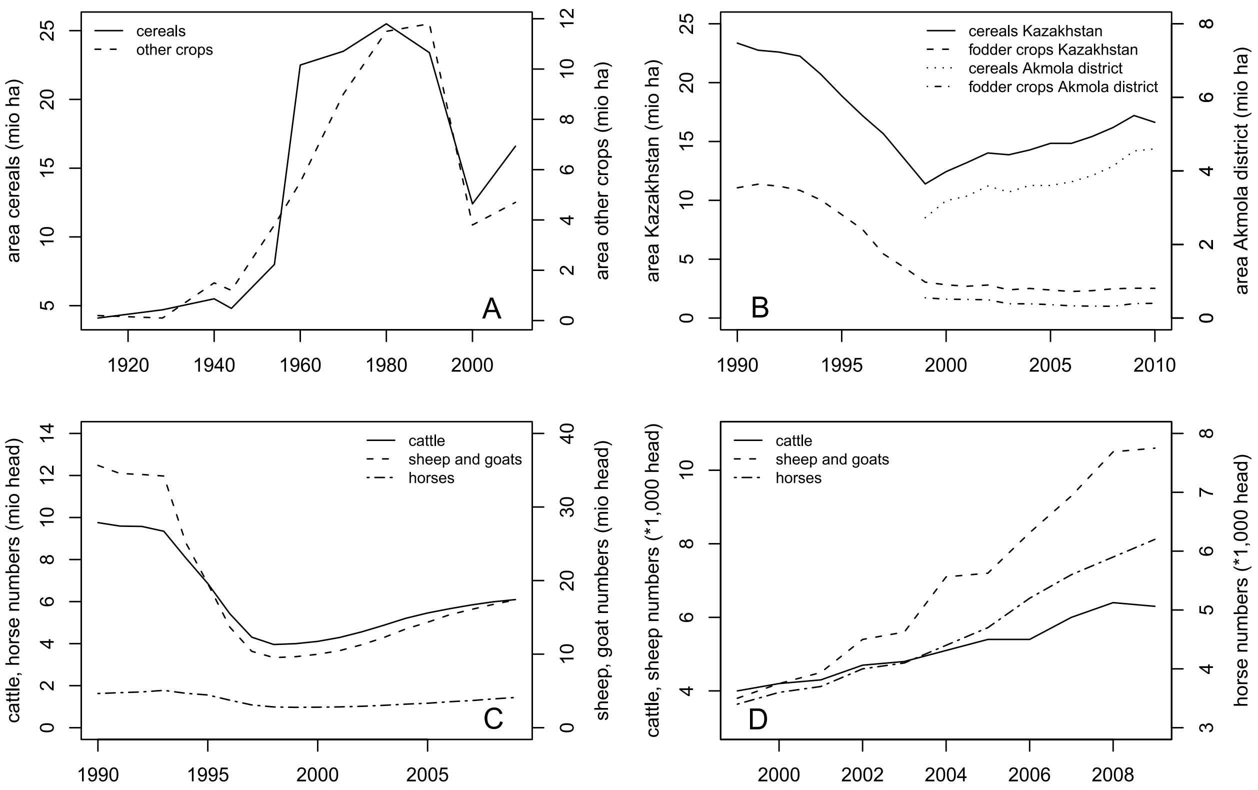

Figure 2. Trends in agriculture in Kazakhstan: (A) area ploughed for cereals and other crops (including fodder grass) 1913 – 2010, Kazakh Soviet Socialist Republic and Republic of Kazakhstan; (B) area ploughed for cereals and fodder crops (mainly fodder grass) since independence, Republic of Kazakhstan and Akmola district; (C) livestock numbers since independence, Republic of Kazakhstan; (D) livestock numbers 1999 – 2010, Korgalzhyn region.

3.2. Bird diversity and abundance

There was a significant difference in species richness between habitats (Kruskal-Wallis ANOVA, $H = 43.00$, df = 5, $p < 0.001$), with ungrazed steppe and arable fields abandoned for longer than 5 years holding the highest number of species (Figure 3). Bird community diversity as measured by the Shannon-Wiener index differed significantly between habitats, with the communities of ungrazed steppe being on average significantly more diverse than those of grazed steppe and arable land (Kruskal-Wallis ANOVA, $H = 14.56$, df = 5, $p = 0.01$, Figure 3).

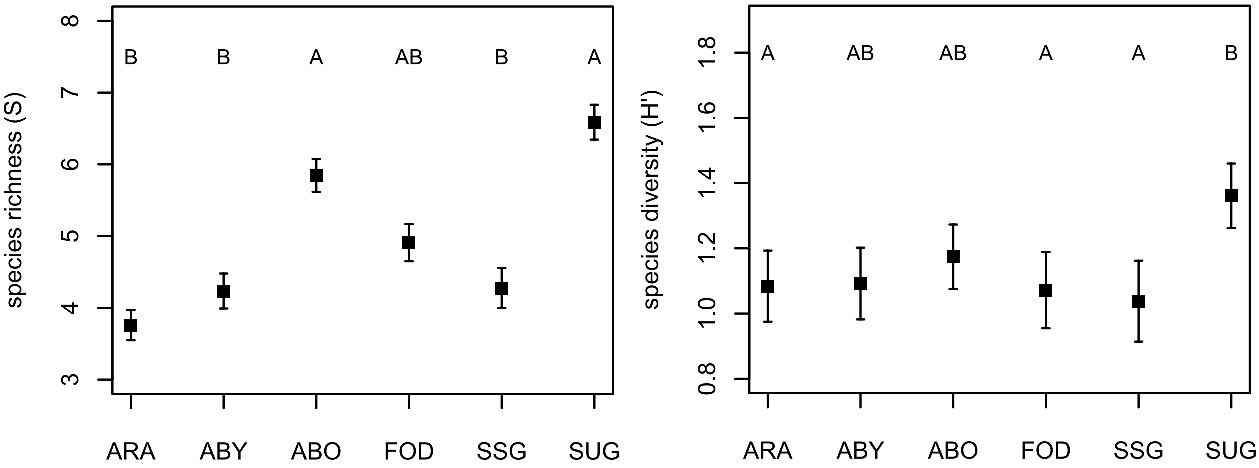

Figure 3. Species richness and diversity (H′) in the studied steppe bird communities (means ± SE). Means with the same letter are not significantly different (α = 0.05). Land-use categories: ARA, arable fields; ABY, recently (1 – 4 years) abandoned cereal fields; ABO, old (5 – 18 years) abandoned cereal fields; FOD, fodder grass; SSG, strongly grazed and overgrazed steppe; SUG, ungrazed steppe.

We had sufficient data to estimate densities for all land-use categories for 15 grassland species, including all biome-restricted species (Table 1). Stubble and ploughed arable fields were used by only a few individuals of most species except Demoiselle Crane *Anthropoides virgo* and Black-winged Pratincole. However, this might be an artefact for the latter species, since arable fields with pratincole colonies were situated significantly closer to water than those without pratincoles (Wilcoxon rank sum test, $W = 526.5$, $p < 0.01$, $n = 161$), and the species is known preferentially to breed close to water (Kamp *et al.* 2009a).

Seven species reached very high mean densities on abandoned wheat fields, including the biome-restricted Black Lark *Melanocorypha yeltoniensis* and the Near-Threatened Pallid Harrier. Long abandoned fields supported very high bird densities, up to 16 times more than the primary habitat of pristine steppe for some species (Table 1). A distinct group of grazing-dependent species reached their highest densities on strongly grazed to overgrazed swards around settlements, including the critically endangered sociable lapwing and the biome-restricted White-winged Lark *Melanocorypha leucoptera* (Table 1).

3.3. Future trends in agriculture

3.3.1. Interviews with farmers

Of the farming companies that were interviewed, 65 % planned to reclaim around 24 210 ha (mean 757 ± 258 SE, range 40 – 8000 ha, $n = 21$ enterprises) of currently abandoned land by 2020 (Figure 4). Assuming that our sample was representative, up to 52 959 ha could be returned to cultivation in the study area (Table 2), leaving 22 % of the area used for cereal crops at the end of the Soviet period (169 246 ha) still abandoned. This confirms the trends apparent in agricultural statistics for the period 2000 – 2010 (Figure 2).

Of the farmers interviewed, 69 % leave fields in fallow rotation (mean 17.7 % ± 2.1 SE of the total farm area, $n = 32$) and do not intend to abandon this practice. At present, agriculture is heavily dominated by wheat cultivation (96.3 % of the area sown). Interviewees planned to diversify crop production (Figure 4) but this will involve trials on 2 – 5 % of the total farm area and commercial success seems unlikely, thus the dominance of wheat in the region seems certain to continue. A significant increase in winter cereals or biofuel crops appears unlikely (Figure 4).

Table 1. Mean bird density (individuals per km² ± SE) for each land-use type. Values on a dark grey background indicate densities of 75 – 100 % of the maximum density reached in this study, those on a pale grey background of 50 – 75 % of the maximum density. The sample size given in brackets after each land-use type refers to the number of transects covered, overall sample size N refers to the number of individuals available for density estimates (* in 87 colonies, ** in 28 colonies).

Species	ARA (*n* = 26)	ABY (*n* = 18)	ABO (*n* = 38)	FOD (*n* = 25)	SSG (*n* = 30)	SUG (*n* = 34)	N	Status
Booted Warbler *Hippolais caligata*	0	12.00±8.19	51.61±12.22	6.10±4.22	1.85±1.36	3.2±1.72	246	L
Quail *Coturnix coturnix*	0	2.47±0.99	4.46±0.74	2.11±0.66	0.33±0.19	0.53±0.25	93	L
Black Lark *Melanocorypha yeltoniensis*	24.07±3.99	73.47±8.79	57.98±6.39	45.13±7.07	1.9±1.02	17.47±3.1	1553	S/R, biome-restricted
Skylark *Alauda arvensis*	19.17±4.18	110.89±17.92	190.74±22.70	144.07±12.75	22.12±6.44	98.03±7.34	3334	S
Yellow Wagtail *Motacilla flava*	0	19.02±12.52	20.54±5.10	21.01±8.38	5.85±2.58	9.13±3.02	301	L
Siberian Stonechat *Saxicola maurus*	0	22.27±14.66	23.16±0.58	24.60±9.82	6.85±3.02	10.69±3.54	166	L
Pallid Harrier *Circus macrourus*	0.02±0.01	0.22±0.07	0.15±0.03	0.10±0.04	0.14±0.04	0.21±0.04	191	L, biome-restricted, NT
Demoiselle Crane *Anthropoides virgo*	0.21±0.05	0.26±0.03	0.17±0.07	0.12±0.05	0.17±0.05	0.22±0.09	266	L, biome-restricted
Short-toed Lark *Calandrella brachydactyla*	45.96±10.59	35.23±13.99	1.17±0.66	6.71±3.84	8.43±3.72	149.87±17.86	737	L
Tawny Pipit *Anthus campestris*	0.31±0.31	0	3.55±1.38	4.06±2.25	2.91±1.18	9.20±2.14	124	L
Steppe Eagle *Aquila nipalensis*	0	0	0.01±0.02	0	0.07±0.01	0.19±0.02	102	L, biome-restricted
Black-winged Pratincole *Glareola pratincola*	7.93±5.58	0	0	0	9.45±2.77	0	3027*	L, biome-restricted, NT
Sociable Lapwing *Vanellus gregarius*	0	0	0	0	2.11±0.61	0	280**	L, biome-restricted, CR
White-winged Lark *Melanocorypha leucoptera*	5.41±2.42	0	0.96±0.96	0	34.37±5.98	1.61±0.73	235	S, biome-restricted
Northern Wheatear *Oenanthe oenanthe*	0.36±0.36	0.46±0.32	0	0	9.18±2.05	0.49±0.26	85	L

Land use categories: ARA, arable fields; ABY, recently (1 – 4 years) abandoned cereal fields; ABO, old (5 – 18 years) abandoned cereal fields; FOD, fodder grass; SSG, strongly grazed and overgrazed steppe; SUG, ungrazed steppe.
Migration strategy and conservation status: L – Long-distance migrant, S – Short-distance migrant, R – resident; IUCN red list categories: CR – Critically Endangered, NT – Near Threatened.

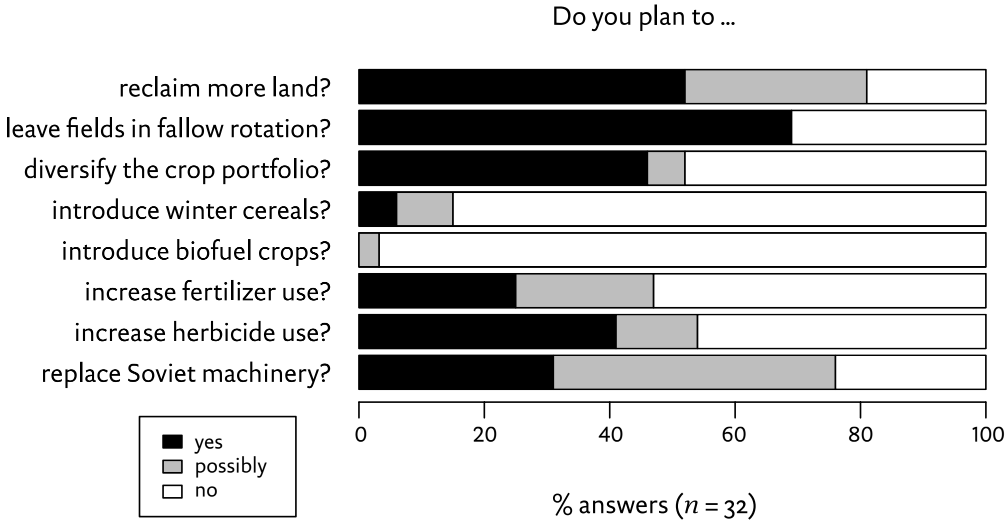

Figure 4. Planned changes in agricultural management, based on interviews with the directors of 32 cereal farming businesses in Korgalzhyn region in October 2010.

Table 2. Projected area change in main land-use categories in Korgalzhyn region until the year 2020. Area change for arable habitats was estimated from quantitative interviews among farming companies, the 33 % reduction target for overgrazed swards was adopted from the regional department of agriculture.

Land-use	Area 2010 (ha)	Area 2020 (ha)	Projected change (%)
Abandoned cereal	81,807	35,652	-57
Abandoned fodder grass	57,534	47,534	-17
Used cereal	87,445	133,600	+53
Fodder grass	15,000	25,000	+66
Overgrazed steppe	25,512	17,093	-33
Moderately to ungrazed steppe	301,993	310,412	+2.7

The use of mineral fertilizer and pesticides is currently rare (applied by 12 % and 37.5 % of the enterprises, respectively, on 17 % and 26.5 % of the land sown in 2010), but might increase in the future (Figure 4). Of the tractors and combine harvesters used by the interviewed enterprises, 74 % and 46 %, respectively were Soviet machinery built before 1991. Most of the respondents are likely to substitute Soviet machinery within the next 2 years for efficiency reasons (Figure 4): grain spill was estimated at 20 – 25 % of the total harvest for Soviet combines, but at less than 5 % for 'western' and newer Russian models.

3.3.2 Interviews with private livestock owners

At present, small-scale subsistence animal husbandry prevails in the study area: 84 % of all cattle, 70 % of all sheep and goats and 72 % of all horses are owned by private households. Only 14 % of the private stock keepers will certainly enlarge their stock numbers and 34 % may possibly do so, 17 % are planning to keep numbers stable and 7 % reducing the number of stock. Overgrazing of communal village pastures was perceived as problematic by 36 % of the telephone interview respondents, as milk and meat quality suffered from the large walking distances (up to 25 km for cattle) that need to be covered daily to reach ungrazed, nutrient-rich vegetation. Nevertheless, currently only 19 % of the villagers transferred all or parts of their stock to remote pastures, with 97 % utilising communal pastures around the settlements.

3.3.3 Semi-structured interviews

The agricultural department considered the reclamation of 50 000 ha abandoned cereal by the year 2020 to be realistic and stated that abandoned land would be reclaimed before new areas of pristine steppe would be ploughed. There are plans by the local administration to promote large cattle factories with up to 20 000 cattle.

Members of the agricultural department considered overgrazing around settlements a serious problem with a large impact on local economy and soil erosion. At present, plans are being developed to reactivate more remote pastures in order to mitigate these negative impacts, with the aim to decrease livestock load on village pastures by one third within the next 10 years. Even with projected increases in both private and commercial livestock, suitable management will ensure that heavy grazing loads are reduced.

3.4 Future changes in bird population size

Based on changes in habitat availability due to changing land-use (Table 2), species currently reaching high densities on abandoned farmland are expected to decline strongly within the next decade, particularly Booted Warbler *Hippolais caligata,* Quail *Coturnix coturnix* and Yellow Wagtail (Figure 5). If destocking plans and better pasture management are realised, this will result in a loss of short-grazed habitat. As a consequence, several species occurring nearly exclusively on overgrazed swards, such as Sociable Lapwing and Northern Wheatear *Oenanthe oenanthe,* are expected to decline strongly as well. Increases were predicted only for Short-toed Lark *Calandrella brachydactyla* and Black-winged Pratincole, species able to breed on arable fields (Figure 5).

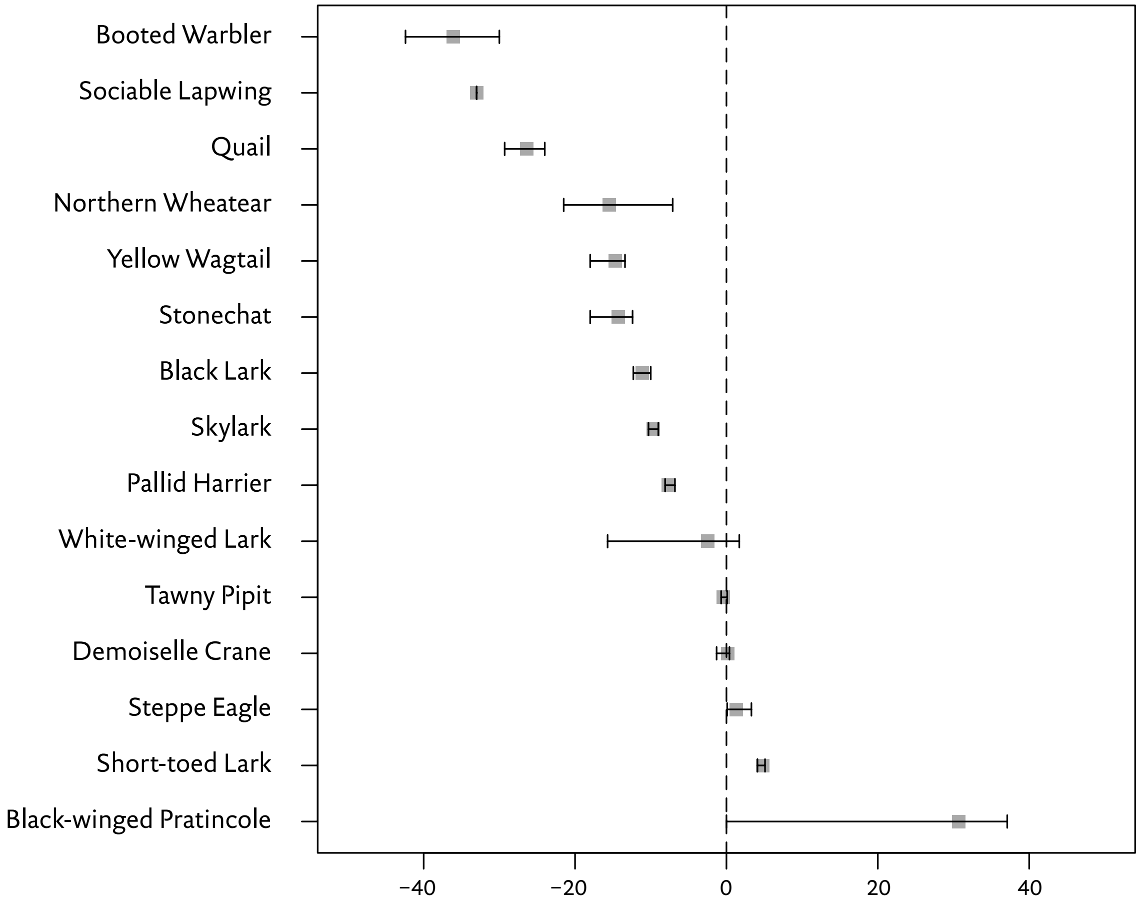

Figure 5. Projected population trends 2010 – 2020 (% change) for 15 steppe bird species under a scenario of maximum reclamation of abandoned land, no new cultivation of pristine steppe and reduction of grazing pressure around settlements of 30 % by 2020. Dots refer to estimates using mean bird densities, confidence intervals were calculated using bootstrapped upper and lower confidence limits of bird density estimates. Note that predictions were based only on change in habitat availability and do not reflect other possibly important changes such as intensification or mechanisation in agriculture.

4. Discussion

Our results suggest that the large-scale abandonment of arable areas and the concentration of domestic livestock led to widespread population increases in grassland birds after the collapse of the Soviet Union in 1991, a trend exactly opposite to that observed across much of Europe (Donald *et al.* 2006) during the same period. However, the ongoing reclamation of abandoned land and a trend towards reducing stock densities are predicted to cause pronounced new declines in a number of steppe species within the next decade.

4.1 Uncertainty in future population estimates

We modelled bird population numbers for 2020 solely as a function of habitat availability and (because of the uniformity of the study system) assumed no strong landscape effects. As we based our predictions on simple extrapolations of observed densities, there was no need to account for density-dependence.

At least 10 % of land reclaimed for arable production is likely to be left in fallow rotation in the near future, so species reaching high abundances in the early stages of abandoned land might decline less than predicted. With increasing livestock numbers and the increasing use of remote pastures, a proportion of the abandoned fields might be used as pastureland leading to an alteration of vegetation structure, but we were unable to gather information on the scale of this process. Potential effects on birds are difficult to predict, but might be positive: there is evidence that moderate grazing levels lead to a faster restoration of steppe vegetation on abandoned fields (Dieterich 2000) and increase invertebrate abundance in grasslands (Kruess & Tscharntke 2002). Black-winged Pratincoles were found nesting in high numbers on recently reclaimed wheat fields, but there is evidence that these habitats act as a sink due to low breeding success (Moseikin *et al.* 2004), thus the predicted increase in numbers might be too optimistic. A projected increase in pesticide application will directly affect birds breeding on arable fields: weed control was identified as a key driver in farmland bird declines in Europe, leading to reduced seed and invertebrate availability and ultimately to low chick survival (Newton 2004). Impacts of increased pesticide use on adjacent grassland habitat and wetlands are possible. An increase in inorganic fertilizer use will lead to denser swards and elimination of broad-leaved plant species through competition, thus also reducing seed availability (Newton 2004). Thus, population declines on arable and adjacent abandoned land might be more severe than predicted. Increasing mechanisation by replacing Soviet machinery with more modern equipment will lead to more efficient harvest and reduced availability of spilled grain. This might negatively affect survival and reproductive success (Gillings *et al.* 2005) – many species currently fatten up nearly exclusively on the large amount of spilled grain on stubble fields in autumn before migrating. For example, densities of four lark species were four to eight times higher on stubble fields compared to any other habitat in October 2010 (R. Urazaliev, unpublished data).

4.2 Transferability and generality of the results

Comparable large-scale abandonment of arable farming and changes in livestock numbers were observed in Ukraine, Russia and Kazakhstan after the collapse of the Soviet Union, thus we consider the situation described here representative for a huge grassland belt across Eastern Europe and Western Asia (Figure 1).

Results of bird censuses in Saratov district NE of Volgograd, Russia match those presented here very closely: arable fields were species-poor and overall bird densities low, intensive grazing led to similarly high densities of White-winged Lark and wheatears as in our study, and densities of Skylark, Stonechat and Booted Warbler were up to 2.5 times higher on long abandoned farmland compared to pristine steppe (Oparin 2008). In Kalmykia (Russia), at the southwestern border of the Eurasian steppes, abandoned arable fields hosted densities of Calandra Lark *Melanocorypha calandra* and Corn Bunting *Miliaria calandra* up to twice those of pristine steppe, especially in the first 2 years after abandonment (Fedosov 2010). The complete recovery to pre-1950 levels of the depleted eastern Little Bustard *Tetrax tetrax* population was attributed to agricultural change (Gauger 2007), as 30 % were found breeding on abandoned wheat fields in the late 1990s (Shlyakhtin *et al.* 2004).

However, trends and patterns might have differed in the Pontic steppes west of the Volga river (cf. Figure 1): In Ukraine, the area ploughed decreased continuously by 21 % after 1990 (State Statistics Committee of Ukraine 2010), but farmland was abandoned mainly outside the steppe zone (Baumann *et al.* 2010 and Charles 2010) and the area sown for cereals, the main crop on productive steppe soils, has increased steadily since 1990 (State Statistics Committee of Ukraine 2010). Livestock numbers collapsed in the 1990s and have not recovered since, unlike in Kazakhstan (State Statistics Committee of Ukraine 2010). Hence, we consider it unlikely that steppe birds in Ukraine enjoyed a period of recovery as in Kazakhstan and Russia.

4.3 Implications for conservation

A significant future loss of grassland bird diversity in Kazakhstan seems inevitable if no remedial action is taken. Approaches to conserve grassland birds have traditionally focused on the retention of near-natural habitat in protected areas and policy interventions to preserve populations remaining in the agricultural matrix after cultivation.

Only 3.9 % of Kazakhstan's steppe area is covered by protected areas (IUCN categories I – IV, UNEP-WCMC 2011). A large, new governmental steppe conservation project, the 'Altyn Dala Conservation Initiative' was recently launched, with the main aim being in situ conservation of grassland habitat by the means of a set of new, interconnected protected areas (Klebelsberg 2008, Figure 1). However, so far the focus of the project is very much on a restoration of threatened ungulate populations, especially the Critically Endangered Saiga antelope *Saiga tatarica* (Singh & Milner-Gulland, 2011). We suggest protected area designation equally considers biome-restricted and globally threatened bird species such as Pallid Harrier, Sociable Lapwing and Black Lark.

Furthermore, the Altyn Dala territory covers only 14 % steppe habitats, with the remainder being semi-desert and desert (Figure 1). Thus, northern steppe parts that are at a higher risk of being claimed for intensifying agriculture due to higher amounts of precipitation will hardly benefit, and additional effort by NGOs and the government to maintain and enhance the set of protected areas in more productive steppe regions across Kazakhstan and Russia is required.

Recent debates on biodiversity conservation on farmland have focused on two competing solutions: wildlife-friendly farming (which boosts densities of wild populations on farmland but may impact agricultural yields) and land sparing (which minimises the demand for new farmland by increasing yields in existing farmland, Green *et al.* 2005). Our study suggests that even at the current relatively low level of farming intensity, with little use of chemicals or winter cropping, the bird biodiversity retained in active arable fields is very low in the steppe zone, whereas abandoned farmland supported higher numbers of some species than pristine steppe. This suggests that a land-sparing approach, i. e. support for the intensification of existing farmland rather than reclaiming abandoned fields, might be the more favourable option. However, rigorous quantitative approaches are needed to evaluate which solution might be more beneficial (Phalan *et al.* 2010).

Finally, grazing management should be monitored carefully in Kazakhstan. Loss of intensively grazed swards could be problematic for several species that rely on heavily grazed areas. Current efforts to reduce overstocking around human settlements will lead to intermediate grazing levels over larger areas, that might be beneficial for other species (e.g. Black Lark). More research is needed to determine grazing levels maximising benefits for biodiversity in the Eurasian steppe zone.

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Appendix

Table S1. Relative abundance of scarce and rare breeding birds observed during walked transect counts, given as number of transects a species was recorded on, separately for each land-use type. The sample size given in brackets after each land-use type refers to the number of transects covered, overall sample size *N* refers to the total number of individuals counted.

Species	ARA (*n* = 26)	ABY (*n* = 18)	ABO (*n* = 38)	FOD (*n* = 25)	SSG (*n* = 30)	SUG (*n* = 34)	*N*	Status
Montagu's Harrier *Circus pygargus*	0	1	0	0	0	2	3	L
Long-legged Buzzard *Buteo rufinus*	0	0	1	0	0	3	4	S
Merlin *Falco columbarius*	0	0	0	0	0	0	1	S
Common Kestrel *Falco tinnunculus*	0	1	1	2	1	5	10	S
Lesser Kestrel *Falco naumanni*	0	0	0	0	1	2	3	L
Short-eared Owl *Asio flammeus*	1	0	0	0	0	1	2	S
Little Bustard *Tetrax tetrax*	0	0	0	1	0	0	1	L, Near Threatened
Hoopoe *Upupa epops*	0	0	0	0	3	0	4	L
White Wagtail *Motacilla alba*	1	0	0	0	3	0	5	S
Bluethroat *Luscinia svecica*	0	1	6	1	2	2	27	L
Barred Warbler *Sylvia nisoria*	0	0	0	0	1	0	2	L
Common Grasshopper Warbler *Locustella naevia*	0	0	1	1	0	0	2	L
Red-backed Shrike *Lanius collurio*	0	0	0	0	2	0	5	L
Twite *Carduelis flavirostris*	0	0	5	1	0	8	37	S
Red-headed Bunting *Emberiza bruniceps*	0	0	0	0	3	0	8	L

Land use types: ARA, arable fields; ABY, recently (1 – 4 years) abandoned cereal fields; ABO, old (5 – 18 years) abandoned cereal fields; FOD, fodder grass; SSG, strongly grazed and overgrazed steppe; SUG, ungrazed steppe. Migration strategy and conservation status: L – Long-distance migrant, S – Short-distance migrant.

CHAPTER 3

Kamp J, Siderova TV, Salemgareev AR, Urazaliev RS, Donald PF, Hölzel, N
(submitted)

Niche separation of larks (Alaudidae) on the drylands of the former Soviet Union: Differential impacts of agricultural abandonment and changing grazing patterns

Agriculture, Ecosystems and Environment *submitted*

Author contributions: JK collected the data, conducted the analysis and wrote the paper.
TVS, AR, RU and PFD provided additional data.
PFD and NH gave advice on sampling design, data analysis and write-up.

Summary

Larks (Alaudidae) are the dominant bird family across the Eurasian steppe zone, which has undergone extensive changes in agricultural management since the dissolution of the Soviet Union in 1991. We assessed the extent to which the distributions of different species of lark vary along the two main agricultural gradients in the steppe and semi-desert zones of Kazakhstan: the intensity of grazing and the time since abandonment of cereal fields.

Vegetation structure and composition varied significantly and non-linearly with time since abandonment, and with changing grazing pressure. The lark species examined responded in non-linear ways to both these gradients and showed a high degree of niche separation, with Black Lark, Calandra Lark and Skylark preferring denser and taller vegetation compared to White-winged and Short-toed Lark.

Lark populations generally are likely to have benefitted from agricultural abandonment and a decline in livestock numbers over large parts of the steppes and semi-deserts of the former Soviet Union. We suggest that an assessment of future changes in steppe bird communities based upon projections of changes in the area of gross habitat types can be improved by a better understanding of the responses of different species to more subtle environmental gradients.

1. Introduction

Changes during the past century in agricultural land-use on the steppes and semi-deserts of the former Soviet Union have been extreme. Most of the western Eurasian steppes (Ukraine and western Russia) were cultivated by the 19th century, but arable farming in the Kazakh Soviet Republic and the steppes of Russian Western Siberia remained relatively restricted until the start of the Soviet 'Virgin Lands Campaign' in 1953 (McCauley, 1976), when within just seven years over 30 million ha of steppe were ploughed, predominantly for wheat cultivation. This area changed little until the economic and social turmoil that followed the dissolution of the Soviet Union in 1991 led to the abandonment of vast tracts of farmland across the steppes of the former Soviet Union (Hölzel *et al.* 2002, De Beurs & Henebry 2004, Charles 2010), the area of abandoned croplands reaching 12 million ha in the year 2000 in Kazakhstan alone (Kazakhstan State Statistics Agency, 2011). Over the last ten years, abandoned farmland has increasingly been reclaimed for cultivation on a large scale, but in 2010 there were still nearly 10 million ha of abandoned cultivation of varying age in Kazakhstan, mostly in the southern steppe zone (Appendix S1).

Livestock management also changed during this period, moving from highly nomadic systems in the 19th century to semi-nomadic approaches in Soviet times to local, year-round concentration of livestock in high densities around human settlements after 1991 (Kerven *et al.* 2006, Kamp *et al.* 2011). Livestock numbers on the steppes of Kazakhstan were high in pre-Soviet and Soviet times, but collapsed after the dissolution of the Soviet Union in 1991, since when they have increased again (Appendix S1).

Wild ungulates once roaming in herds of millions over the steppes are now nearly extinct in the region (e.g. Kulan *Equus hemionus*, Goitered Gazelle *Gazella subgutturosa*) or reduced to tiny populations (e.g. Saiga antelope *Saiga tatarica*) due to overhunting and poaching (Milner-Gulland *et al.* 2001, Robinson & Milner-Gulland 2003, Singh *et al.* 2010; Appendix S1), greatly reducing their previously profound impacts on the steppe ecosystem.

These changes have had pronounced impacts on a unique suite of steppe grassland species, many of them threatened and endemic to the extensive natural grasslands of central Eurasia (Sanchez-Zapata *et al.* 2003, Tella *et al.* 2004, Gauger 2007, Oparin 2008, Terraube *et al.* 2008, Kamp *et al.* 2009, Fedosov 2010, Singh *et al.* 2010, Singh & Milner-Gulland 2011).

In a previous analysis, we related steppe bird numbers to broad habitat categories to make predictions about the impacts of past and future land use change, concluding that recent socio-economic changes have affected bird populations over huge areas (Kamp *et al.* 2011). Here, we assess the drivers of these broad-scale patterns by assessing niche separation in the numerically dominant bird family in the region, the larks (Alaudidae) along the main agricultural gradients. The Eurasian steppes and semi-deserts are a region of high lark diversity with six genera and 13 species, and constitute a worldwide distributional hostpot for the genus *Melanocorypha* (Suárez *et al.* 2009). Larks reach extraordinarily high densities and biomass totals: for northern Kazakhstan, Ryabov (1974) estimated that just four lark species comprised 75 % of total avian bird biomass in tall- and short-grass-steppes (89 % on arable land and 50 % in semi-deserts, respectively). The steppes of Kazakhstan and Southern Russia host two breeding endemic larks, the Black Lark *Melanocorypha yeltoniensis*, which is mostly confined to more productive grasslands, and the White-winged Lark *M. leucoptera*, which reaches highest densities in semi-deserts and dry steppes (Dolgushin *et al.* 1970). Larks therefore represent a key component of steppe bird communities and can be considered reliable indicators of fine-scale environmental variation across these huge areas of natural and modified open habitats (Moreira 1999, Serrano & Astrain 2005, McMahon *et al.* 2010, Reino *et al.* 2010). We relate the distribution and abundance of these key steppe species to fine-scale habitat and land-use variables, allowing a more precise assessment of the proximate determinants of steppe bird communities than is possible by comparing only gross habitat types and so permitting a better understanding of the impacts of current and future land-use change in the region. We focus on the responses of five species (Calandra Lark *Melanocorypha calandra*, White-winged Lark, Black Lark, Short-toed Lark *Calandrella brachydactyla* and Skylark *Alauda arvensis*) to the two main ecological gradients in agricultural landscapes of Central Kazakhstan: grazing intensity and time since abandonment of arable fields. Our specific aims were to assess the extent to which successional changes in abandoned agricultural fields and grazing intensity influenced vegetation structure, and how this in turn influenced the structure of bird communities.

2. Material and methods

2.1 Study areas

Productive and abandoned arable farmland was surveyed in 2009 on four former state farms in the Korgalzhyn region of Akmola district in Central Kazakhstan (50°35′ N, 70°00′ E). The area is situated in the dry steppe ecozone, the most southerly region farmed for cereals in Soviet times (McCauley 1976; Figure 1). The region lies at the southern edge of the Kazakh Steppe ecoregion and encompasses large areas of pristine short-grass steppe. Soils are humous-rich Kastanozems, and the main vegetation communities are dominated by the feather grasses *Stipa lessingiana* and *S. capillata*, the native fescue *Festuca sulcata* and wormwoods *Artemisia*. The study region is situated in a zone of 'high-risk agriculture', where regular droughts adversely affect yields (Dieterich 2000). Approximately 42% of the region's land area was cultivated for arable farming in Soviet times (1959 – 1991), but large tracts of farmland were abandoned after 1991 (Kamp *et al.* 2011). Cereals dominate agriculture, with rain-fed wheat grown on about 95% of utilised farmland. Information on the age of abandoned fields was obtained from Dieterich (2000), interviews with local land owners and Landsat 7 ETM+ scenes. The year of the last ploughing could often be established precisely, but might be slightly inaccurate (± 2 years) in a few cases.

Grazed land was surveyed in two adjacent regions in the Torghay area of Kostanai district (Amangeldinskii and Dzhangeldinskii raions), Central Kazakhstan in 2010, situated in the desert steppe and semi-desert ecozones (Figure 2). For surveys, we chose five larger settlements hosting up to 4 000 cattle and sheep and two small livestock stations herding flocks of around 300 sheep and 100 cattle. The region is characterised by human depopulation of large areas after the collapse of the Soviet Union and dramatic decreases in livestock numbers. The remaining livestock are housed overnight within villages and towns and driven out in flocks each day to graze nearby. Soils are humous-poor Kastanozems, often heavily saline. The main vegeta-

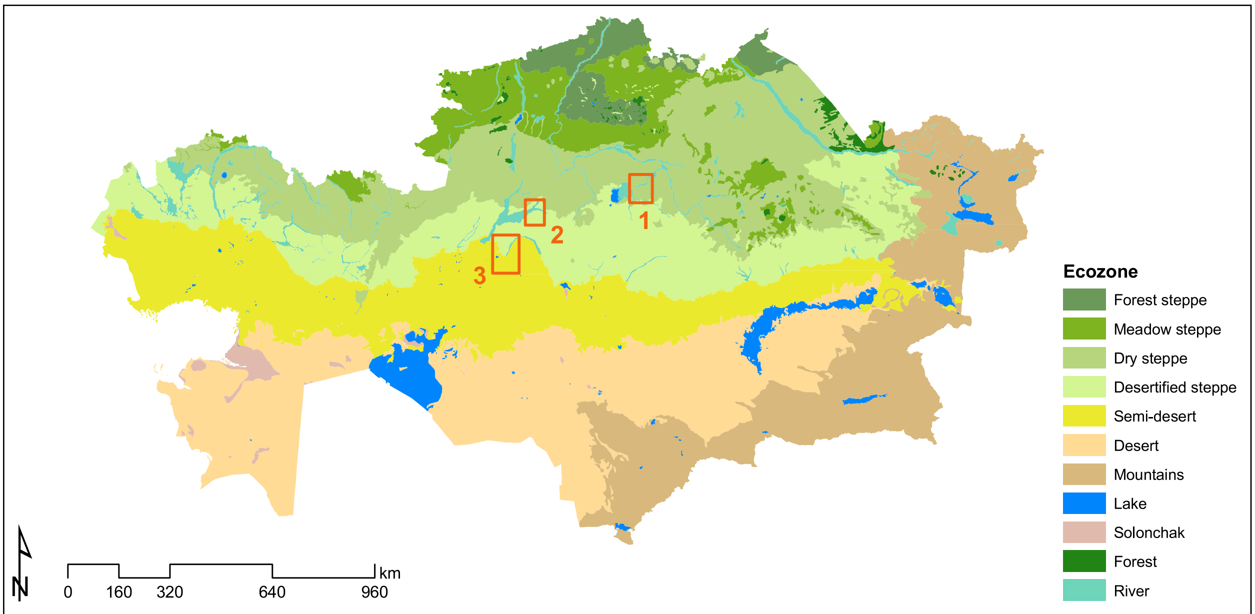


Figure 1. Main ecozones of Kazakhstan and study areas: 1) Korgalzhyn region, Akmola district (mainly arable), 2) Amangeldinskii raion, Kostanai district (dry and desertified steppe pastures) and 3) Dzhangeldinskii raion, Kostanai district (semi-desert pastures). Ecozone data provided by UNEP/GEF.

tion communities are dominated by various wormwood species and feathergrasses (mainly *Stipa sareptana* and *S. pennata*).

2.2 Bird surveys

In the arable study area, a contiguous block of fields was selected around a random start point on each former state farm. Within these blocks, 106 line transects of 500 m length were walked every 2 km using a regular sampling design, with the starting point being always situated 1 km away from the field corner at the centre of the field edge. Twenty-six transects fell on fields still used for wheat cultivation. During the survey they were either covered in stubble (first round of counts in May), or the wheat plants were just emerging (mean vegetation height 19.7 cm ± 1.17 SE, second round of counts in late May/ beginning of June). Twenty-three transects fell on fields with Crested Ryegrass *Agropyron cristatum* sown for cattle fodder. Fodder grass fields were used for winter hay production when livestock numbers were high in Soviet times. After the collapse of the Soviet Union, they were increasingly not resown (but still mown, cf. Appendix S1). This has led to changes in the sward structure and plant community, with the sown grass gradually being invaded by steppe plants.

The remaining 57 transects fell on abandoned cereal fields of various age (maximum 16 years). Mean field size was 410 ha ± 126.8 SD (range 130 – 766 ha), with no delineating structures such as fences or hedgerows, thus creating vast expenses of similarly structured landscapes. Used fields were treated as 'year zero' in the gradient of abandonment. Some of the abandoned and fodder grass fields were grazed with rather low stock densities.

In the area dominated by livestock grazing, 15 survey routes were placed around the seven settlements, starting at the settlement edge and extending radially for 9 km. This end distance was chosen because sheep move up to 4 and cattle up to 9 km away from the settlement during the day (Robinson *et al.* 2003, Kamp *et al.* 2009), suggesting the highest impact of grazing fell within this distance.

Two to three routes were placed around each settlement running parallel to the main routes of livestock herding. At each of these routes, we stopped every 1 km and walked a total of 136 transects of 1 km length perpendicular to and centered on the route.

Bird counts in the arable study area were conducted between 05 May and 23 May 2009 and repeated between 25 May and 13 June 2009. In the pasture areas, only one count was coducted per route, between 07 and 26 May 2010. Surveys started at dawn and finished before 10 a.m., when bird activity declined markedly. Distance sampling was used to account for varying detectability between habitats and species (Buckland *et al.* 2001). We estimated the perpendicular distance to each bird (excluding flyovers) within distance bands of 0 – 5 m, 5 – 10 m, 10 – 25 m, 25 – 50 m, 50 – 100 m, 100 – 200 m, and 200 – 500 m. Laser range finders (Bushnell Scout 1000) were used to calibrate distance estimation.

2.3 Recording of habitat variables

We recorded a number of variables to characterise vegetational gradients on arable and grazed land that mirror vegetational succession on abandoned arable land and grazing impact by domestic livestock on uncropped land: total vegetation cover (i.e. cover of bare soil), cover of grasses, cover of feather grass (*Stipa spec.*), cover of woody wormwood (mainly *Artemisia austriaca, A. schrenckii* and *A. pauciflora*), maximum vegetation height and cover of livestock dung. Grass and *Artemisia* cover are good indicators of grazing intensity, as the latter is rather unpalatable and bitter and remains whereas grasses are selected by the animals (Bock *et al.*, 1984, Yunusbaev *et al.* 2003). On abandoned fields, the cover of weedy wormwood species (mainly *A. dracunculus* and *A. marschalliana*) was also recorded, as these are dominant in most areas. Variables were selected on the basis of our own experience of the area and literature references (Dolgushin *et al.*, 1970).

In the arable areas, recording plots of 2 x 2 m were set up every 100 m along each transect (total 636 plots) and the values for all habitat variables were averaged for analysis over these six plots. In the grazed areas, due to logistic constraints, only one, larger recording plot of 10 x 10 m was centered on each transect. Coverage was estimated by eye to the nearest 10 % (nearest 1 % when below 10 % cover).

2.4 Estimating livestock densities

In our study, we focused on cattle and sheep as these are concentrated in dense flocks in small areas and are thus likely to alter vegetation strongly, unlike the herds of semi-wild horses that wander the steppe unshepherded (Yunusbaev *et al.* 2003). The cattle and sheep of each household in the settlements are collected by shepherds in the early morning, driven radially out of the settlements in flocks for grazing and herded back each evening. To quantify the spatial extent of domestic livestock movements and grazing patterns, and derive an index of livestock density, GPS data loggers (i-gotU tracking devices, Mobile Action Technology Inc.) were attached to at least one cow and one sheep (total 11 cattle and 7 sheep) at every settlement of the Torghay study area using specially designed neck collars. As the animals are kept in relatively tight flocks, the position of the tagged animal was considered representative of that of the whole flock. The loggers were programmed to fix the animals' position every five minutes from 6:00 until 18:00 h for five days within the same period that habitat variables were recorded on the ground. These point data were subsequently downloaded and processed in ArcGIS 9.3. To estimate grazing intensity, the settlements were buffered with concentric bands of 1 000 m width and the number of logger fixes falling into these distance categories was calculated, corrected for the area of each annulus. The number of fixes per annulus was divided by the total number of fixes and so scaled to 1 for each logger seperately. We assumed that the time spent in every distance band, and thus the density of fixes logged to the GPS per annulus, reflected grazing intensity. There was no evidence for preferred resting sites of the animals, so we assumed that time spent resting (and thus creating a large number of points in one area despite low grazing activity) was equal for all distance bands.

2.5 Data analysis

2.5.1 Bird density estimates

Population densities were modelled as a function of distance to observer for each species separately in program DISTANCE 6.0 (Thomas *et al.* 2010) to account for varying detection probability across species and habitats. We assessed detection models with half-normal and hazard-rate shapes and identified those performing best using Akaike's Information Criterion (AIC, Buckland *et al.* 2001, cf. Appendix S2). In a few cases where the data were slightly spiked (i. e. more observations than expected in the first distance category), we preferred half-normal over hazard-rate shapes although the latter had lower AIC values associated – this resulted in more conservative density estimates. As bird detections were assigned to a relatively small number of distance bands, we did not employ series expansions to avoid overfitting. For the 2009 data, detections from the higher count of each species across the two surveys of each transect were included.

2.5.2 Habitat modelling

As species – habitat relationships are often nonlinear, we used a Generalized Additive Model (GAM) framework to relate bird densities to habitat variables. All specified GAMs were constructed using a quasi-poisson approach with a log-link to account for non-normality of the data and varying degrees of overdispersion. The study sites in the grazed study area were spread over a large area and showed variation in vegetation and substrate, thus site (defined as block of fields in the arable area and village in the grazed areas) was included as a fixed factor in all models.

Univariate models were first built for all species and predictor variables. We specified GAMs with cubic spline smoother values of 3 and 4 (Wood 2004) and selected the value with the lower associated Quasi-AIC (corrected for small sample size, $QAIC_C$) for further modelling. Smoothing parameters were estimated using the generalized cross validation method (Wood 2004). All univariate relationships were plotted with standard errors and inspected visually. Variables emerging as significant predictors of species densities at a level of $p < 0.05$ were included in multivariate GAMs. As we had little prior information to produce meaningful sets of candidate models, we built multivariate models containing all possible combinations with a maximum of three variables at any time, using the one of a pair of correlated (Spearman's $r \geq 0.7$) variables that had a higher p-value in univariate models. To select the most informative, models were then ranked by their $QAIC_C$ and Akaike-weights (w_i) calculated. The models whose weights summed up to a value of 0.95 were considered as an informative set (Burnham & Anderson 2002).

To assess whether species overlapped in their niches with respect to the recorded habitat variables, we fitted generalized additive mixed models (GAMMs) that included all explanatory variables as covariates, species as a fixed factor and transect as a random effect to a combined dataset containing the densities of all species on all transects.

In order to evaluate the relative importance of each habitat variable, we additonally constructed algorithmic models of variables influencing lark density using Random Forests (RF). RF are based on classification and regression tree analysis (Breiman 2001). They are used increasingly in ecological modelling (e.g. Oppel *et al.* 2009; Wei *et al.* 2010) as an alternative to frequentist methods due to a number of advantages over classical statistical methodes, namely their ability to handle large numbers of intercorrelated predictor variables, to produce robust rankings of variable importance, and their usually superior model fit compared to traditional methods such as Generalized Linear Models (Elith *et al.* 2006; Prasad *et al.* 2006; Peters *et al.*, 2007). We specified full models containing all predictor variables and site for each species separately and set the number of regression trees to grow to 1 500, with three variables randomly sampled at each split.

All analyses were conducted in R 2.13.1 (R Development Core Team 2011) using the packages mgcv (Wood 2011) and randomForest (Liaw & Wiener 2002). $QAIC_C$ values were extracted using a function implemented in package MuMIn (Barton 2011).

3. Results

3.1 Vegetation characteristics of arable land and pastures

At the arable site, total vegetation cover on cereal fields increased over time since abandonment from 10 % in the first year to around 60 % on fields abandoned 8 years and longer, i. e. younger fallow fields had on average much more bare ground. The cover of grasses (mainly *Festuca sulcata* and *Stipa lessingiana*) remained very low until year 11 after abandonment but increased to over 20 % afterwards (Appendix S3). A similar pattern emerged for woody *Artemisia* species also covering large areas in natural steppe (mainly *A. austriaca, schrenckii* and *pauciflora*), whereas the cover of weedy *Artemisia* (mainly *A. dracunculus* and *marschalliana*) increased to year 8, but then greatly decreased. Vegetation height increased to around 60 cm in year 3, remained rather stable until year 10, but then decreased, so that very old fields had vegetation as short as very young ones. This was probably mainly caused by a gradual substitution of tall, weedy *Artemisia* species by lower steppe bunchgrasses (*Stipa lessingiana* and *Festuca valesiaca*, Appendix S3). Fodder grass fields were similar in their vegetation structure to older abandoned wheat fields, with a mean vegetation cover of around 60 %, high grass cover (mainly *Agropyron cristatum*) and low cover of *Artemisia*. Fodder grass fields were grazed by horse and cattle in very low densities (but higher than on abandoned wheat fields) (Appendix S4).

At the sites grazed by sheep and cattle in the Torghay study area, total vegetation cover increased constantly along the grazing gradient from around 10 % at the settlement edge to around 30 % at 9 km, indicating a very high proportion of bare ground within 1 km of the settlement. Grass cover and cover of woody *Artemisia* (*A. austriaca, pauciflora* and *semiarida*) also increased along the gradient, but showed a less pronounced pattern indicating patchiness of grazing. Maximum vegetation height was lowest within 2 km of the settlements and increased significantly with distance (Appendix S5).

3.2 Grazing intensity around settlements

Livestock density was highest within 2 km of the settlement edge and decreased markedly beyond 3 km. Areas more than 6 km away were not grazed or stocked with extremely low cattle densities (Figure 2D). The maximum distance animals moved from settlements was 9.8 km for cattle and 7.6 km for sheep.

3.3 Drivers of lark density on arable and abandoned arable land

Species was a highly significant predictor ($p < 0.001$) in a GAMM relating lark densities to all habitat variables, suggesting significant differences in realized niches.

Skylark and Black Lark densities increased with increasing age of the abandoned wheat fields up to a maximum around year nine, but then decreased again (Figure 2A), suggesting an ecological optimum in medium to old abandoned fields. Short-toed Larks reached highest abundances on stubble fields and recently (< 3 years) abandoned fields, and avoided older fallow fields (Figure 2A). White-winged Larks occurred on stubble fields in very low densities (overall mean $\hat{D}$ = 0.02 birds / ha ± 0.01 SE, n = 86 transects), and avoided abandoned fields after the first year of abandonment. On fodder grass fields, Skylark and Black Lark densities were similar to those of old abandoned wheat fields (0.45 birds / ha ± 0.07 SE and 1.44 ± 0.12 SE), whereas Short-toed Lark densities were very low (0.06 ± 0.04 SE) and no White-winged Larks were observed.

Variables retained in the multivariate GAMs with highest weights suggested a similar preference of Skylark and Black Lark for taller and denser vegetation (highest densities at around 60 % cover and 60 cm vegetation height), and an avoidance of grazed areas in Black Lark. Short-toed Larks avoided grassy areas and areas with a vegetation height over 30 cm and preferred areas with a high proportion of bare ground as found on stubble fields and young stages of abandonment (Table 1, Figure 3A). Skylarks seemed to prefer areas with intermediate grass cover, while both weedy and woody *Artemisia* cover seemed positively to influence Skylark and Black Lark, but not Short-toed Lark numbers (Table 1, Figure 3A). All multivariate GAMs explained a high amount of deviance (47.7 – 69.9 %) when compared to the respective null models (Table 1).

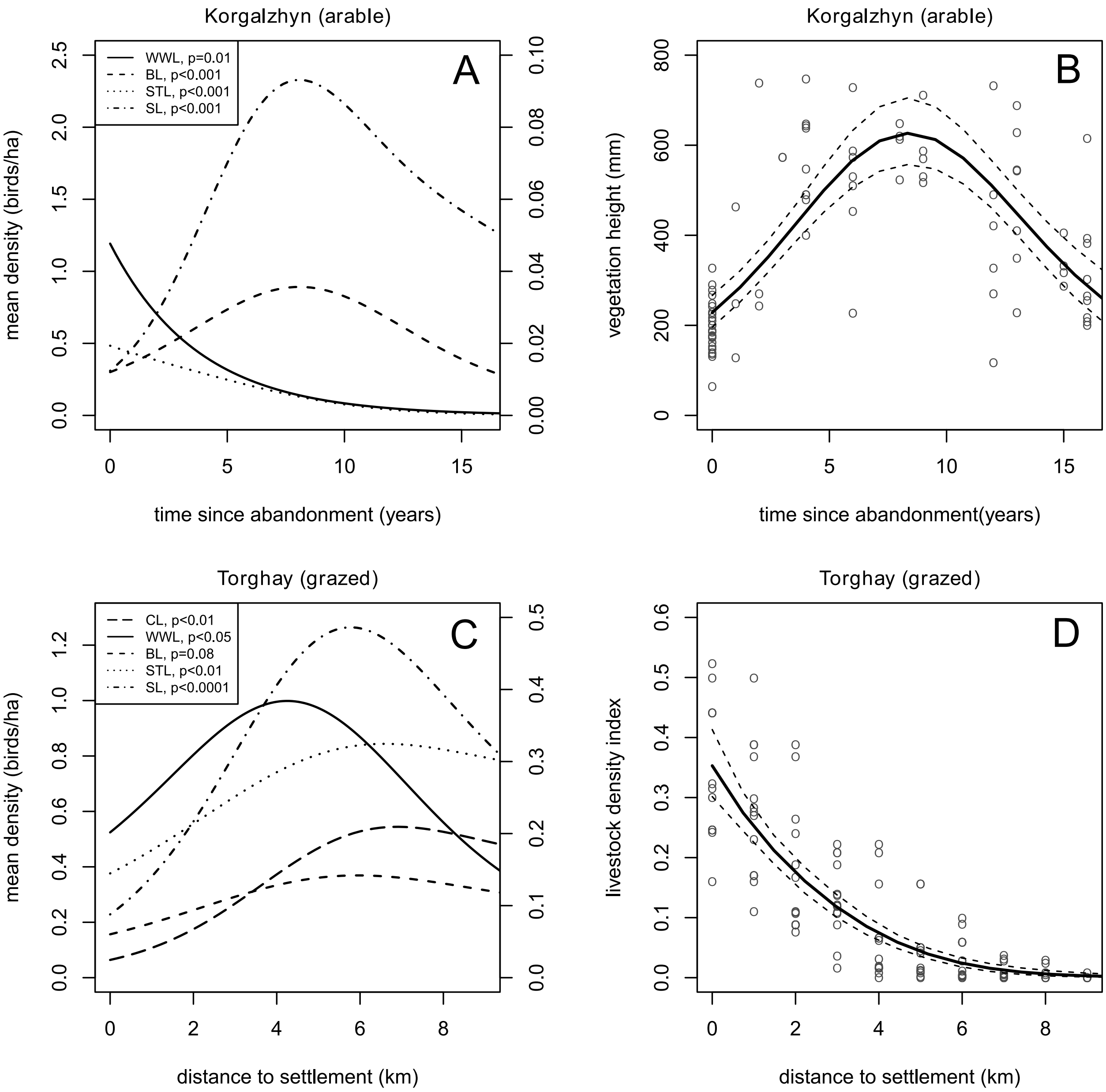


Figure 2. Visualisation of univariate Generalized Additive Models (GAM) of lark densities along a gradient of time since abandonment of arable fields (A, Korgalzhyn area) and grazing intensity (C, Torghay area, expressed as distance to settlement). Plots B and D show key drivers of lark density in the studied systems. In plot A, densities of White-winged Lark are plotted on the right axis, those of the remaining species on the left axis. In plot C, densities of Short-toed and Skylark are plotted on the left axis, and those of the remaining species on the right axis. Year zero in the age of abandonment gradient refers to cultivated arable fields.

Table 1. Models relating lark densities on abandoned fields to environmental variables. All models whose weights sum up to 0.95 are given. No multivariate models were constructed for White-winged Lark due to low sample size, Calandra Larks do not occur in the study area. The shape of the univariate responses is indicated by + (positive response), – (negative response) and 0 (humped relationship). Site was included as fixed factor in all models.

	Model	Intercept	Total plant cover	Cover of grasses	Cover of weedy *Artemisia*	Cover of woody *Artemisia*	Maximum vegetation height	Cover of animal dung	% Deviance explained	$QAIC_C$	$\Delta QAIC_C$	w_i
Black Lark	1	-0.691					+		47.7	114.0	0.000	0.334
	2	-0.685					+	-	48.4	115.5	1.514	0.157
	3	-0.653	+				+		47.9	115.6	1.616	0.149
	4	-0.680			+		+		48.4	115.6	1.625	0.148
	5	-0.669			+		+	-	49.2	117.0	2.992	0.075
	6	-0.649	+				+	-	48.5	117.1	3.095	0.071
	7	-0.642	+		+		+		49.3	117.2	3.203	0.067
Short-toed Lark	1	-2.131		-			-		61.5	116.2	0.000	0.581
	2	-2.266	-	-			-		61.0	116.9	0.686	0.412
Skylark	1	-0.224	+			0	+		69.9	123.6	0.000	0.572
	2	-0.139	+	0			+		68.9	125.1	1.454	0.276
	3	-0.197	+		+		+		68.3	127.8	4.131	0.072
	4	-0.250		0	+		+		67.5	128.9	5.249	0.041

Table 2. Models relating lark densities along a grazing intensity gradient to environmental variables. All models whose weights sum up to 0.95 are shown. The shape of the univariate responses is indicated by + (positive response), – (negative response) and 0 (humped relationship). Site was included as fixed factor in all models.

	Model	Intercept	Distance to village	Total plant cover	Cover of grasses	Cover of woody *Artemisia*	Maximum vegetation height	Cover of dung	Livestock density	% Deviance explained	$QAIC_C$	$\Delta QAIC_C$	w_i
Calandra Lark	1	-1.989					+		-	34.2	75.5	0.000	0.417
	2	-2.051			+		+		-	38.4	75.5	0.042	0.408
	3	-2.185			+				-	34.0	77.3	1.788	0.171
White-winged Lark	1	-3.677	0	0		+				49.3	153.0	0.000	0.809
	2	-3.759		0		+				45.5	157.2	4.172	0.100
	3	-3.358	0	0						44.5	158.7	5.716	0.046
Black Lark	1	-2.460			+					12.7	145.7	0.000	0.507
	2	-2.514			+		+			12.8	147.0	1.333	0.260
	3	-2.590					+			11.0	147.8	2.086	0.179
	4	-2.413								7.96	150.1	4.458	0.055
Short-toed Lark	1	-1.696	+							35.0	146.4	0.000	0.357
	2	-1.615	+					-		35.8	146.8	0.428	0.288
	3	-1.675	+	+						35.1	148.2	1.842	0.142
	4	-1.604	+	+				-		35.8	148.7	2.365	0.109
	5	-1.551						-		32.0	150.9	4.498	0.038
	6	-1.521		+				-		32.8	151.2	4.870	0.031
Skylark	1	0.142	+		0	0				73.0	156.0	0.000	0.826
	2	-0.532	+		0		0			72.3	160.6	4.523	0.086
	3	-0.176			0	0	0			71.7	160.7	4.647	0.081

In agreement with the GAMs, vegetation height and total vegetation cover were the most important variables explaining density differences in RF models (Figure 4). The proportion of variance explained by RF models was 32.0 % for Black Lark, 20.0 % for Short-toed Lark and 48.6 % for Skylark. Prediction accuracy of RF models as measured by the relationship of predicted vs. observed densities was excellent with high R^2 values ranging from 0.91 (Black Lark and Short-toed Lark) to 0.93 (Skylark) (Appendix S6).

3.4 Drivers of lark density on pastures

Species was a highly significant predictor ($p < 0.001$) in a GAMM relating lark densities to all habitat variables, suggesting significant differences in realized niches. Densities of all species initially increased with increasing distance from settlement (Figure 2C) suggesting a strong influence of grazing, which was confirmed by the selection of grazing-related variables in habitat models for all species. White-winged Lark and Skylark numbers reached a peak at different intermediate distances and declined markedly thereafter (Figure 2C). Distance to settlement was a significant predictor for all species except Black Lark (marginally significant), which occurred only in low numbers in the study area (Figure 2C). However, livestock density as estimated by data from GPS loggers was a significant predictor in univariate GAMs only for Calandra Lark and Skylark, probably reflecting varying shapes of the grazing intensity function across settlements.

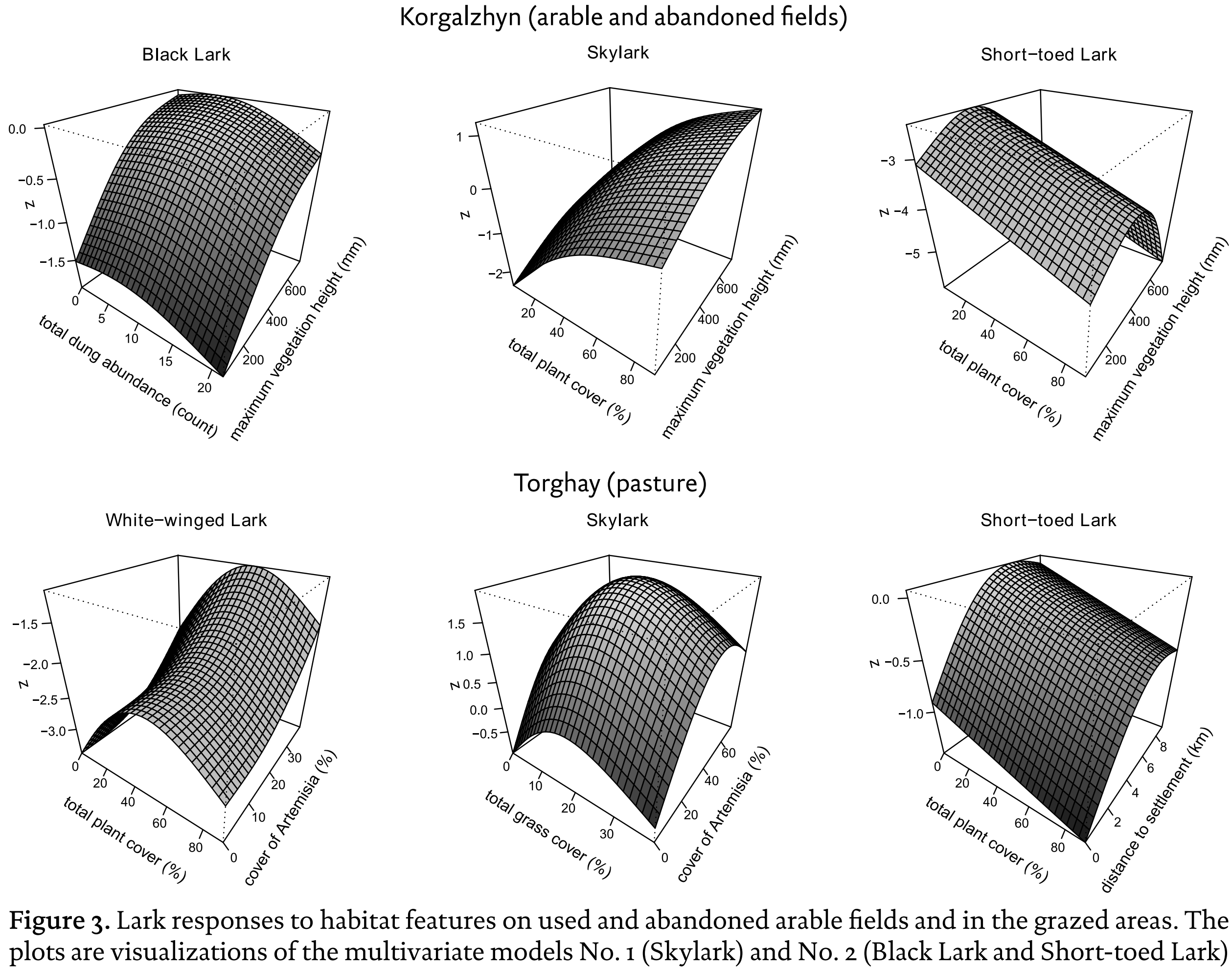


Figure 3. Lark responses to habitat features on used and abandoned arable fields and in the grazed areas. The plots are visualizations of the multivariate models No. 1 (Skylark) and No. 2 (Black Lark and Short-toed Lark) in Table 1 and models No. 1 (White-winged Lark and Skylark) and No. 2 (Calandra Lark) in Table 2. Values on the z-axis are plotted on the scale of the linear predictor, not the response variables. All variables of the models not included in the plots were held fixed.

Variables retained in the multivariate GAMs with highest weights suggested a strong influence of grazing on all species, with avoidance of strongly grazed areas and a preference for tall and dense vegetation in Calandra Larks, an optimum at around 40 % vegetation cover and a high proportion of woody *Artemisia* in White-winged Larks, and a preference for very grassy patches interspersed with *Artemisia* in Skylarks (Table 2, Figure 3). Short-toed Lark numbers decreased with increasing plant cover. Black Larks appeared to prefer grassy areas as Skylarks did, but the explanatory power of the models was very low throughout (Table 2).

RF models were largely in agreement with the GAMs and suggested a high influence of total vegetation cover, grass cover and vegetation height on Skylark abundance, a very strong influence of livestock density on Calandra Lark densities and high importance of woody *Artemisia* for White-winged Lark (Figure 4).

RF models explained a high proportion of variance for Skylark (73.7 %), but rather little for Short-toed Lark (24.51 %), White-winged Lark (24.09 %) and Calandra Lark (6.51 %). Prediction accuracy of RF models as measured by the relationship of predicted vs. observed densities was excellent, with R^2 values ranging from 0.86 (Calandra Lark) to 0.95 (Skylark) (Appendix S6).

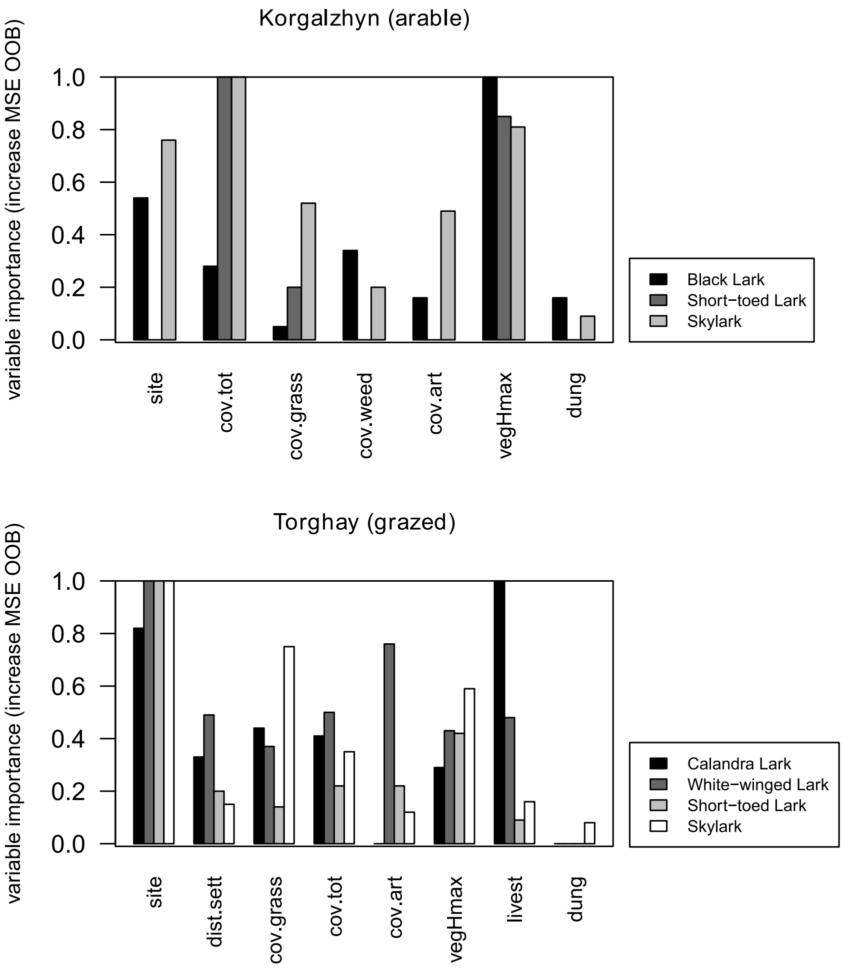


Figure 4. Relative importance of environmental variables in order of their relevance to increase accuracy of a random forest model, scaled to 1 for the most important variable for each species. Site was included in all models. Abbreviations: cov.tot = total vegetation cover, cov.grass = grass cover, cov.weed = cover of weedy *Artemisia*, cov.art = cover of woody *Artemisia*,vegHmax = maximum vegetation height, dung = dung density index, dist.sett = distance to nearest settlement, livestock = livestock density index.

4. Discussion

4.1 Niche separation in larks in relation to land-use

Our results suggest that separation of realised niches in larks is pronounced in arable areas of the steppe zone that are characterised by a high degree of abandonment. In grazed areas of the dry steppes and semi-deserts, niches overlapped more.

While we are not aware of any previous studies examining habitat preferences of White-winged and Black Larks, research from transformed open landscapes in Europe seems to suggest a high transferability of our results for the remaining species. Lark distribution and abundance in agricultural and pastoral landscapes of Europe (where the size of fields of equal crop type and management regime is only a fraction of those in our study area) is mainly governed by landscape context and fragmentation (Baldi *et al.* 2005, Morgado *et al.* 2010, Reino *et al.* 2010, Vögeli *et al.* 2010), but differences in vegetation have been used repeatedly to explain lark distribution and abundance on smaller scales. Calandra Lark densities in the steppes of European Russia were highest in ungrazed steppes with tall bunchgrasses and a diverse flora (Fedosov 2010), whereas densities on the Iberian peninsula tended to increase with vegetation height (Morgado *et al.* 2010). Short-toed Lark presence in Spain was related to low grazing pressure and a high cover of small xerophytic scrubs, whereas there was no significant influence of vegetation height (Suárez *et al.* 2002). Overall, the species seems to be a generalist compared to other larks in their natural arid habitats (Serrano & Astrain, 2005), which might explain the lack of any vegetation variables in all but our poorest models (Table 2).

Skylark territory density on British farmland reached a maximum at a vegetation height of 55 cm (Donald *et al.* 2001), very similar to the 60 cm in the abandoned arable areas of our study. Densities peaked at 27% bare ground on set-aside in the UK (Henderson *et al.* 2001), again remarkably close to the 30% bare ground cover estimated for our arable study area. A combination of open areas used for foraging and denser vegetation conceiling nests, as found in both set-aside in Europe and abandoned fields, seems to be characteristic of landscapes harbouring the highest Skylark densities in Europe.

Habitat niche separation in the studied lark communities is probably driven by differences in bill and foot structure: Bill length increases from a mean of 11.2 mm in Short-toed Larks to 18.9 mm in Calandra Larks (Glutz v. Blotzheim *et al.* 1987 – 1999), and bill shape varies strongly across the species considered here suggesting different food niches. Larks living in densely vegetated habitats (such as abandoned fields) have significantly longer toes and claws and thus larger footspans than those inhabiting bare substrates such as stubble fields or strongly grazed pastures (Table 3; Green *et al.* 2009), which has been suggested to facilitate movement over uneven or unstable vegetation ('snowshoe effect'; Green *et al.* 2009).

Table 3. Length (mm) of the hindclaw, hindtoe and total foot length (length of all toes summed) for four steppe larks (data from Green *et al.* 2009). Measurements from museum specimens, no measurements were available for White-winged Lark.

	Hindclaw	Hindtoe	Total foot length
Calandra Lark	16.1	11.6	70.6
Black Lark	8.0	7.8	47.1
Short-toed Lark	14.9	12.0	79.0
Skylark	15.3	9.9	78.0

4.2 Implications of land use change for lark population sizes

Black Larks and Skylarks clearly profited from post-Soviet agricultural abandonment, whereas White-winged Larks and Short-toed Larks vanished immediately or shortly after cereal fields were abandoned due to unsuitable vegetation structure. This suggests that in arable areas, Black Lark and Skylark populations increased between 1991 and 2000, but have been declining since, as large-scale reclamation of abandoned fields has started (Kamp *et al.* 2011) and fields become older, whereas the trend was probably the opposite in White-winged and Short-toed Larks.

Livestock numbers in the Soviet Union crashed in the early 1990s (Robinson & Milner-Gulland, 2003; Appendix S1) and spatial grazing patterns shifted: during the Soviet era, Kazakhstan (where not farmed) was covered by a dense network of livestock herding stations, on the steppes and semi-deserts usually situated at small dams, purpose-drilled wells or natural lakes and rivers. Robinson *et al.* (2003) suggests that herds travelled rarely further than 4 km from their base, but given considerable seasonal movements and the sheer number of flocks, large parts of the country were grazed by domestic livestock, and considerable numbers of Saiga antelope (Robinson & Milner-Gulland 2003; Appendix S1). Since the break-up of the Soviet Union, livestock are largely owned privately. During the 1990s the water infrastructure across most of the country collapsed due to a withdrawal of state subsidies, and village communties were unable to maintain dams and wells. This, and a lack of fuel and machinery for stock transport led to a cessation of seasonal movements and an increase in plant biomass, vegetation height and vegetation cover across large parts of the steppes and semi-deserts (e.g. De Beurs & Henebry 2004, Dubinin *et al.* 2011).

Our results suggest that this development was largely beneficial for Calandra, Black and Short-toed Lark, which seem to thrive best where grazing intensity is very low or livestock are absent completely. Skylarks would have benefitted in sparsely-vegetated semi-desert areas where grassy patches are actively selected by domestic stock, but possibly not in the steppe zone as they showed an association with certain low stock densities. White-winged Larks might have declined in the steppe zone, since on high-load pastures *Artemisia* species become dominant due to being relatively unpalatable, and they showed a clear association with moderate stock densities.

Overall, our data suggest that there have been considerable population increases in the Eurasian steppes since the mid-1990s in all lark populations considered here, most pronounced for Calandra Lark, Black Lark and Skylark. There are few quantitative data to confirm this trend, but Belik (2000) concludes from extensive line-transect counts in the SW Russia steppes and semi-desert that declining lark populations reached a low in the end 1980s and recovered since. For the Calandra Lark, Fedosov (2010) noted a massive increase on the steppes of Russia between 2000 and 2010 and relates that to the collapse in livestock numbers.

However, reclamation of abandoned fields to cereal agriculture is likely to continue in Kazakhstan (Kamp *et al.* 2011). This might be beneficial for White-winged and Short-toed larks if the current low-input cereal systems are maintained, but forecasted agricultural intensification might devalue this habitat by increased pesticide and fertiliser use. Black Lark and Skylark populations are likely to suffer from reclamation of abandoned land.

Livestock numbers are still very low in our study region compared to the Soviet era (Appendix 1), but strong increases have been observed since 2 000 in other parts of the Russian and Kazakh steppes and semi-deserts, and this trend is likely to continue (Dubinin *et al.* 2011; Kamp *et al.* 2011; Appendix 1). Milner-Gulland *et al.* (2006) modelled pastoralist behaviour in Kazakhstan and suggested a return to Soviet practices (i.e. decentralized stock-keeping with flocks outposted to natural and artificial water sources) when stock numbers continue to increase, ultimately leading to heavier grazing of more steppe areas. This might be beneficial for White-winged Larks and Skylarks, but will almost certainly lead to lower densities of Calandra, Black and possibly Short-toed Larks. Increasing livestock numbers will also lead to a resowing of fodder grass (Kamp *et al.* 2011), with potential changes to sward structure and vegetation that might affect Black Lark and Skylark, both abundant in this habitat.

Saiga antelope population levels are still very low in Kazakhstan, but have started to recover (Appendix 1). In Kazakhstan, large-scale conservation action (mostly protected area development and anti-poaching campaigns) is targeted at the species within the framework of the multi-stakeholder 'Altyn Dala ('Golden Steppe') Initiative' (Singh & Milner-Gulland, 2011), so future population recovery seems likely.

5. Conclusions

The common approach of classifying steppe and farmland birds into broad habitat categories for management planning will not account for the fact that densities vary strongly within habitats. Instead more complex models are needed to guide management decisions on the landscape level. Even then, there will be no all-win situations, as each species requires a different set of habitat components, a situation commonly encountered in both arable and pastural systems (e.g. Suárez-Seoane *et al.* 2002; Baldi *et al.* 2005; Arthur *et al.* 2008; Johnson *et al.* 2011).

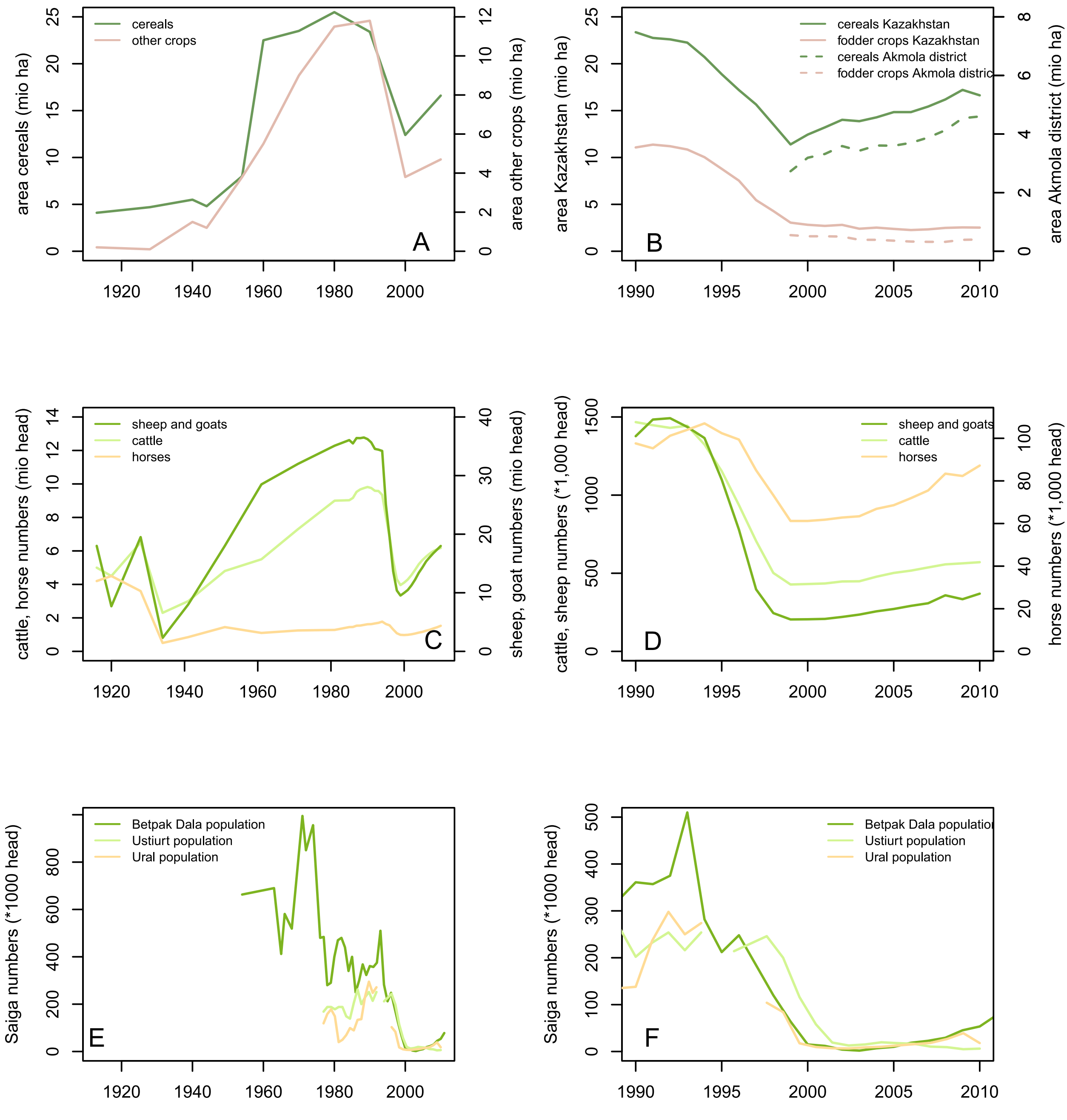
Two approaches seem advisable to maintain suitable habitat and thus high densities of larks in steppe ecosystems of Eurasia: Leaving single fields fallow for a period of several years on a rotational basis in the arable matrix (e.g. as an agri-environmental measure) would provide habitat of high value for a species of high conservation concern, the Black Lark, and boost Skylark densities. The large protected areas currently being designed in the framework of the Kazakh government's Altyn Dala Conservation Initiative should include areas with different levels of grazing intensity by livestock, and a monitoring of the impact of increasing Saiga antelope populations.

A reduction in the current heavy grazing levels around settlements seems debatable – while larks would certainly benefit, there might be negative implications for other species preferring short-cropped swards such as the critically endangered sociable lapwing *Vanellus gregarius* (Kamp *et al.* 2009, 2011). The interactions between wild ungulates, domestic livestock and steppe birds remain insufficiently studied for the Eurasian steppes, but with an ongoing recovery of Saiga antelope populations, vegetation and bird numbers are likely to change again.

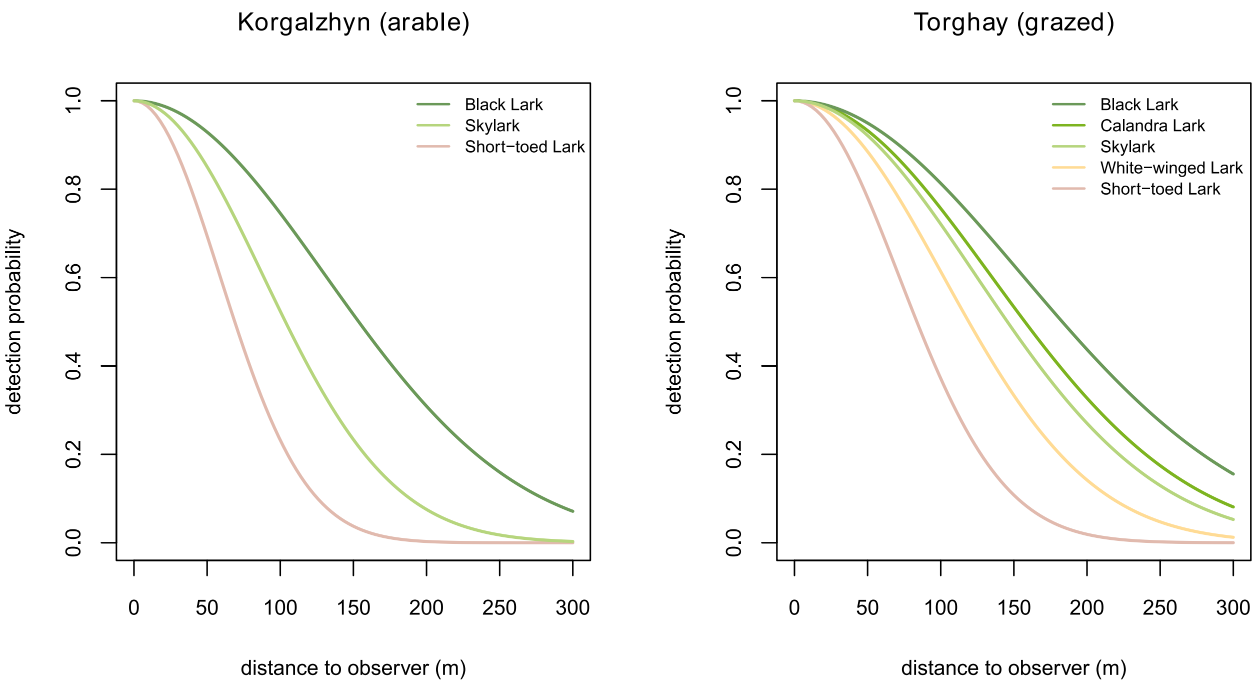
Acknowledgements

We thank Michael Brombacher, Vladimir Chapurin, Daniyar Dozzhanov, Talgat Kisebaev, Sayat Mukhtarov, Henrietta Pulikova, Alexander Putilin, Sergey Sklyarenko, Alena Shmalenko, Mark Underhill and Steffen Zuther for help with data collection and logistics in the field. We are grateful to Rhys Green for providing measurements for claw and toe length in the studied species. Comments of Steffen Oppel significantly improved an earlier draft of the manuscript. Fieldwork and analysis were funded by the UK government's Darwin Initiative (Project Ref-No. 18 004).

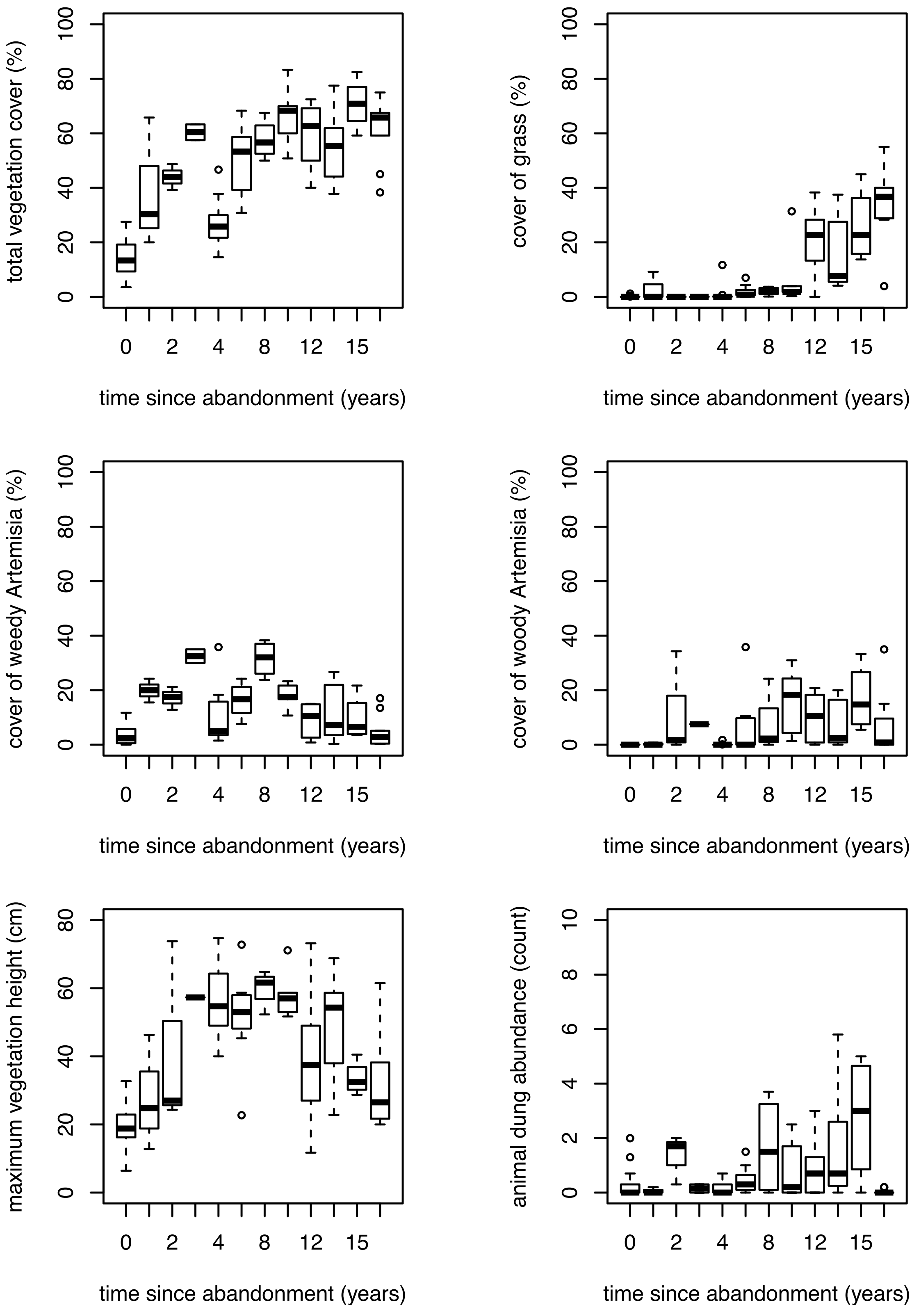
Appendices



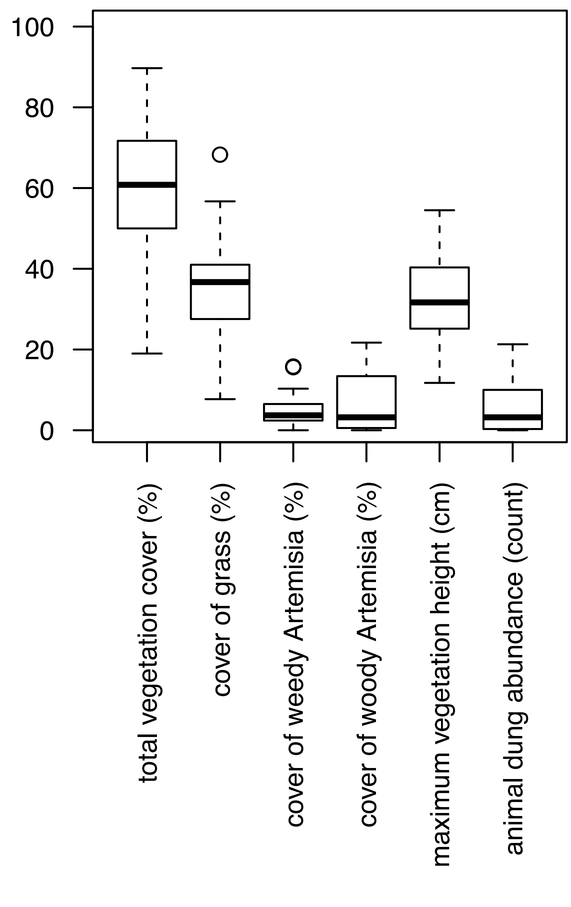
Appendix S1. Trends in agriculture and numbers of wild and domestic grazers in Kazakhstan: A) area ploughed for cereals and other crops (including fodder grass) 1913 – 2010, Kazakh Soviet Socialist Republic and Republic of Kazakhstan; B) area ploughed for cereals and fodder crops since independence, Republic of Kazakhstan and Akmola district; C) livestock numbers 1915 – 2010, Kazakh Soviet Socialist Republic and Republic of Kazakhstan; D) livestock numbers since independence, Kostanai district; E) unsmoothed Saiga antelope count data 1960 – 2010. Sources: A)–D): Kazakhstan state statistics agency (2011), E) and F): Institute of Zoology, Almaty (in litt., 2011) and ACBK (S. Zuther in litt., 2011). All figures show unsmoothed trends and contain missing values for a number of years.



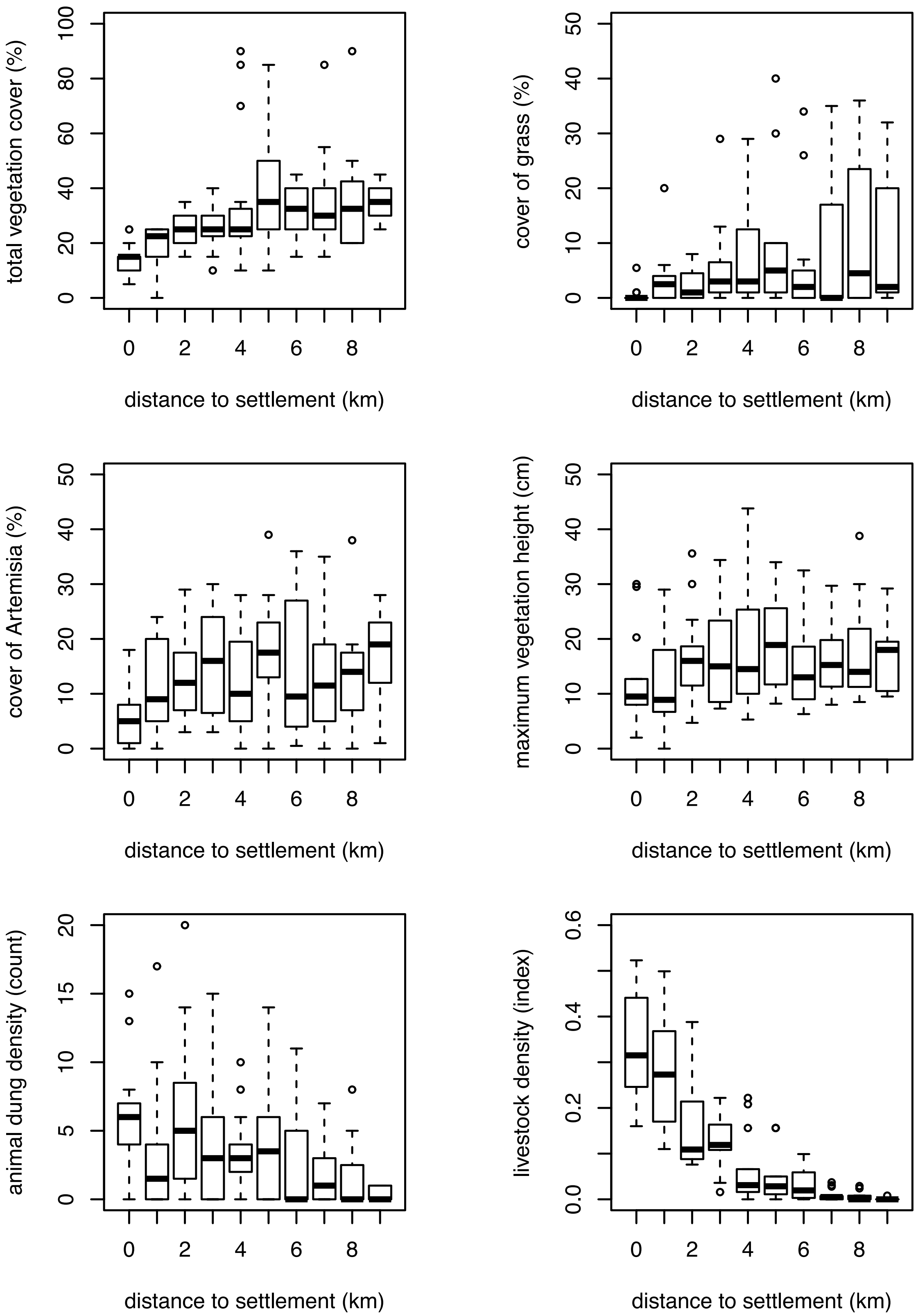
Appendix S2. Modelled detection probabilities for all species (half-normal models without series expansions). Detection probability decreases similarly with distance to observer for the same species in the arable and the grazed areas, but seems to decline steeper overall in abandoned arable habitats, probably due to taller and denser vegetation and thus poorer visibility of birds on the ground.



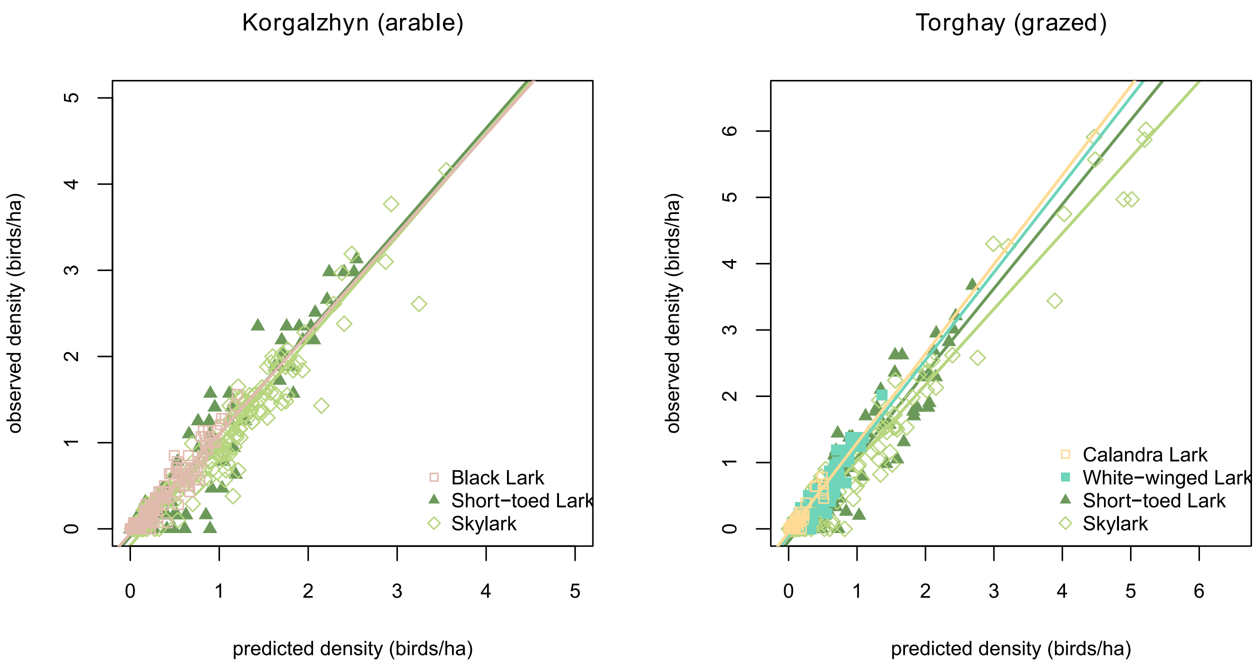
Appendix S3. Boxplots of main habitat variable values along a gradient of time since abandonment (means of 6 sample plots on 83 transects, Korgalzhyn study area.) Year 0 represents fields still used for wheat farming.



Appendix S4. Boxplots of main habitat variable values on fodder grass fields (means of 6 sample plots on 23 transects, Korgalzhyn study area).



Appendix S5. Boxplots of main habitat variable values along a gradient of grazing intensity (n = 136 sample plots), pooled over all settlements (Torghay study area).



Appendix S6. Plots of observed against out-of-bag predicted lark density from Random Forest models four five species on abandoned fields and grazed steppe. Lines represent standard linear regressions.

CHAPTER 4

Kamp J, Sheldon RD, Koshkin MA, Donald PF, Biedermann R (2009)

Post-Soviet steppe management causes pronounced synanthropy in the globally threatened Sociable Lapwing *Vanellus gregarius*

Ibis 151: 452 – 463

Author contributions: JK collected the data, conducted the analysis and wrote the paper.
RDS, MAK and PFD provided additional data on nest sites from earlier years and livestock density.
PFD and RB gave advice on sampling design, data analysis and write-up.

Summary

Habitat associations and distribution of breeding Sociable Lapwings were examined in 2004 – 2008 in central Kazakhstan to develop and assess hypotheses relating to the species' decline and high conservation threat status. At a landscape scale, breeding colonies were strongly positively associated with villages and rivers. Habitat suitability models had very high predictive power and suggested that only 6.6 – 8.0 % of the 30 000-km² study area was potentially suitable for Sociable Lapwings. Models developed to describe the spatial distribution of nests in one region of Kazakhstan in one year predicted well the distribution of nests in another region, suggesting good generality. At a colony scale, nests were most likely to be found in the most heavily grazed areas, with a high cover of animal dung and bare ground. Despite the low density of human settlements in the study area, most Sociable Lapwing nests were < 2 km from a village. Patterns of grazing were assessed by fitting GPS loggers to cattle. There was a strong positive correlation around villages between grazing intensity and the density of Sociable Lapwing nests, with clear evidence of a threshold of grazing density that needs to be reached before birds will breed. This high degree of synanthropy, perhaps unique in a critically endangered bird, is likely to result from post-Soviet changes in steppe management and offers both threats and opportunities to the species' conservation.

1. Introduction

The Sociable Lapwing *Vanellus gregarius* is a semi-colonial wader whose breeding distribution is confined to the Pontian (Eurasian) steppe belt. In common with other steppe species (e.g. Pallid Harrier *Circus macrourus* and Black-winged Pratincole *Glareola nordmanni*), its numbers have undergone a severe decline over the last 100 years. Sociable Lapwing numbers collapsed after the 1950s, and the decline accelerated in the 1990s (Ryabov 1974, Gordienko 1991, Eichhorn & Khrokov 2002). The species vanished from nearly half its former range during the 20th century, becoming extinct in Ukraine in the 1960s (Dolgushin 1962) and west of the Ural River (including European Russia) in the 1980s (Tomkovich & Lebedeva 2004). Few quantitative data on the decline of the breeding population are available, but post-breeding maximum flock size on the breeding grounds decreased from several thousand birds around 1900 to rarely more than a thousand in the 1950s, and only tens of birds between 1969 and 2000 in Kazakhstan (Plotnikov 1898, Dolgushin 1962, Gordienko 1991). As a result of these declines and an assumed population size of 200 – 600 breeding pairs, the species' IUCN threat status was uplisted to Critically Endangered in 2004 (Birdlife International 2008). Within its current stronghold in Kazakhstan, breeding colonies are scattered across huge areas, making precise estimation of population size difficult. Surveys conducted in 2005 – 2008, however, suggest a larger world population than previously feared, with a current crude estimate of 5 600 pairs (Sheldon *et al.* 2006).

Reasons for the decline remain unclear, but have been linked to low productivity on the breeding grounds (Watson *et al.* 2006), perhaps arising from changes in habitat suitability. The collapse of collectivist farming after the break-up of the Soviet Union has resulted in major changes in steppe use and management. Also, the hunting to near extinction of native grazers, especially the Saiga antelope *Saiga tartarica* (Milner-Gulland *et al.* 2001), may have led to a reduction in the availability of grazed steppe favoured by many species. However, not enough was known about habitat use and distribution of Sociable Lapwings to assess the possibility that these changes have contributed to observed declines. Recent reports from the Middle East suggest that hunters kill significant numbers at stopover sites (S. Jbour pers. comm.). This might have influenced population trends, and habitat changes in the wintering areas might also be implicated (Tomkovich & Lebedeva 2004).

We studied breeding habitat and nest-site selection of the species using a two-level habitat suitability modelling approach combined with spatial analysis of nest-site distribution and grazing patterns of domestic livestock. Our aim was to develop predictive models and link these with past and likely future changes in land use to assess the reasons for past declines and to forecast future population trends.

2. Methods

2.1 Study areas

Data on Sociable Lapwing abundance and distribution were collected between 2004 and 2008 in a study area in the Lake Tengiz depression centred on the settlement of Korgalzhyn, 120 km southwest of Astana, Kazakhstan. The study area covered approximately 30 000 km² and stretched between 49°40′ – 50°55′ N and 68°38′ – 70°59′ E. Habitat suitability models were developed using nest-sites found and habitat data collected on 9 000 km² of this study area in May and June 2006. The models were tested for spatial transferability in an area of approximately 12 000 km² in the Irtysh region of northeast Kazakhstan's Pavlodar province, which was surveyed for Sociable Lapwing colonies in 2007. This area is situated between the lower Irtysh river at the settlement Akku (= Lebyazhe, 51°28′ N, 77°46′ E) and the Russian border (53°47′ N, 75°03′ E).

The Korgalzhyn study area is characterized by flat short-grass steppe and cereal fields in the north and hilly semi-desert in the south. Land-use is restricted to livestock rearing and wheat cultivation, with about 80 % of all arable fields having been abandoned since Kazakhstan's independence in 1991. The area holds hundreds of both fresh and saline lakes (Solonchaks), the largest being the saline Lake Tengiz with an area of 1 380 km². The Pavlodar study area is dominated by the Irtysh river. The adjacent landscape on both sides of the river is characterised by herb-rich tall-grass steppe and small birch forests (transition to West Siberian Forest Steppe).

2.2 Habitat suitability modelling

2.2.1 Sampling design

Surveys for Sociable Lapwing colonies and nests were conducted throughout the Korgalzhyn study areas between April and June in 2004 – 2008, and in the Pavlodar study area in 2007. Habitat data were collected between 10 May and 16 June 2006 in the Korgalzhyn study area. In all years, all previously known breeding sites of Sociable Lapwing were surveyed, information on which was available from local databases and expert communication (Watson *et al.* 2006). Furthermore, we cold-searched large areas of pristine steppe and fallow fields. Observers regularly stopped at vantage points and surveyed the surrounding area using a telescope, and additionally searched for Sociable Lapwings when driving transects at low speed (c. 10 – 20 km / h) across all habitat types. In 2006, the total length of survey transects across the area was 1 176 km. These transects connected 109 points chosen randomly across all habitat types and were surveyed at least once in the second half of May, when birds are most active. Using telescopes, Sociable Lapwings can be detected over large distances in the flat and uniform steppe landscape, up to some kilometres for flying birds and group-displaying males in good light conditions. After locating territorial birds, observations from a distant vantage point or car facilitated location of incubating females and nests.

In 2006, breeding habitat selection was studied at both landscape and colony scales across the Korgalzhyn study area. The sample unit at the landscape scale was the breeding colony. A colony was defined as a site with an aggregation (inter-nest spacing < 500 m) of at least two breeding pairs at least 3 km away from the next breeding site. The spatial extent of each colony was determined by buffering each nest-site cumulatively with r = 500 m in ArcView 3.2a GIS. This distance was chosen because adults during the incubation period rarely moved more than 300 – 400 m away from the nest and thus this distance should represent the area used around a particular nest-site (see also Watson *et al.* 2006 for colony structure). Within 30 colonies, variables were measured at a randomly chosen nest-site representing 'presence'. These data were compared with habitat data collected at 109 points randomly selected (representing 'absence') across the whole study area for analysis at the landscape scale. Random points were automatically generated in the GIS using a random point generator and were constrained not to fall within colony borders or on open water.

The sample unit at the colony scale was the single nest. At 17 colonies across the Korgalzhyn study area, habitat data collected at nest-sites were compared with those at randomly chosen points within the borders of the colony representing habitat availability. Random points were constrained not to fall within 25 m of a nest. In total, habitat data were collected at 78 nest-sites and 262 randomly chosen absence points, resulting in a total sample size of 340 sample points for analyses of habitat selection at the colony scale. Nests found later than 25 May were excluded to avoid the inclusion of second clutches from breeders which failed during a first attempt and which might have differed in selected habitat and introduced pseudoreplication.

2.2.2 Recording of habitat variables

The choice of habitat variables was hypothesis-based and informed by the literature and our own experience with the species from 2004 and 2005 (Table 1). Plant composition and cover was recorded at 2 × 2 m sample plots, centred on each nest-site or random point. Cover was estimated to the nearest 5 %. Vegetation height was measured at every nest-site and every random point on two scales. We distinguished between maximum vegetation height, defined as the height of the tallest plant within each plot, and modal

Table 1. Overview of all recorded habitat parameters.

Code	Description
elev[a]	Elevation above sea level (m)
slope[a]	Slope (°)
asp[a]	Aspect (arccos/arcsin-transformed)
dist.riv	Distance to nearest river (m)
dist.lake	Distance to nearest standing water feature (m)
dist.wat	Distance to nearest water feature (m)
dist.col[a]	Distance to nearest Sociable Lapwing colony (m)
dist.nest[b]	Distance to nearest Sociable Lapwing nest (m)
dist.rook	Distance to nearest rookery (m)
dist.sett	Distance to nearest settlement (m)
dist.veg[b]	Distance to the nearest vegetation patch of significantly different height (± 20 cm difference) (m)
vegH.max	Maximum vegetation height (mm)
vegH.mod	Modal vegetation height (mm)
cov.art	Cover of wormwood *Artemisia* spp. (%)
cov.stip	Cover of feather grass *Stipa spp.* (%)
cov.fest	Cover of fescue *Festuca spp.* (%)
cov.grass.tot	Total grass cover (%)
cov.herb	Cover of herbaceous plants (other than grasses) (%)
cov.ML	Cover of mosses and lichens (%)
cov.veg	Total vegetation cover (= cover of bare ground) (%)
cov.dung	Cover of dung (%)
dung.tot[a]	Dung abundance (strip transect count)
soil.type	Soil type
soil.surf	Soil surface structure

[a] Landscape scale only.
[b] Colony scale only.

vegetation height, defined as the height of the majority of plants. Soil type and soil surface structure were recorded as one of seven substrate classes. As dung is a very good correlate of grazer density (Laing *et al.* 2003), each nest-site and random point was characterized by the cover of dung in the same way as the plant cover estimates. This proved an ineffective method at larger scales, as livestock is comparatively mobile and dung density low, so at the landscape scale, all livestock dung piles were counted over a strip transect of 25 × 2 m both to the west and east of each nest-site and random point. Altitude was recorded at every point from a handheld GPS unit, and slope and inclination were measured with a clinometer and a compass, respectively.

For spatial analysis, Soviet topographic maps (scaled 1 : 100 000) of the whole study area (last updated 1989) were rectified and stored in the GIS. A rectified Landsat 7 ETM+ satellite image (issued 9 July 2002) was saved as an overlay to identify landscape changes after the map issue. Based on this data, a digital map was created containing information on the main land-use types, rivers, lakes and infrastructure. Values for distance variables were calculated using the extensions 'nearest features' and 'distance matrix' for ArcView 3.2a (Jenness 2004, 2005).

2.2.3 Data analysis

Habitat models were developed using binary logistic regression at both landscape and colony levels. Univariate models for all variables were built first using the 'logistf' package for S-Plus 6.1 by Heinze & Schemper (2002). To avoid the inclusion of spurious variables in multivariate models, each univariate model was internally validated by boot-strapping with 300 iterations (Verbyla & Litvaitis 1989). For each boot-strap iteration (resampling of the dataset without replacement), deviance reduction compared to the non-boot-strapped model was recorded and a likelihood-ratio test (LRT) conducted. Variables were included in the further multivariate modelling process (see below) only if the boot-strap-LRT was significant ($p \leq 0.05$) for at least 95% of the boot-strap iterations. We included second-order terms in all univariate models to allow for unimodal relationships (Austin 2002). Where both sigmoid and unimodal responses were significant, we chose the one with the lower p-value for multivariate modelling, usually accompanied by better fit of the univariate model (Strauss & Biedermann 2006).

For multivariate modelling, we built models for all possible combinations of four, three and two variables in an automated process using a self-programmed script for S-Plus 6.1. Including more than four variables in the same multivariate model would have led to over-parametrisation (Guisan & Zimmermann 2000). To reduce multicollinearity (Graham 2003), only combinations of variables with $r_S < 0.5$ were allowed to appear in the same model. As we intended to achieve parsimonious models, LRTs were conducted for every model to assess whether they were better than (or just as good as) any model with one less variable (Ferrier *et al.* 2002). Additionally, we assessed whether Nagelkerke's R^2 (R^2_N) of a boot-strapped model (mean of 300 iterations) was ≥ 0.3 (Strauss & Biedermann 2006). R^2_N describes model calibration and refinement (Nagelkerke 1991). If both requirements were fulfilled, the model was considered adequate.

Because many adequate models were obtained, an information theoretic approach (Burnham & Anderson 2002) was used to select those that were most informative. For each candidate model, the Akaike information criterion (AIC) was calculated to assess how well models performed in the trade-off between model fit and model complexity. We used the corrected value AIC_C, as recommended when sample size is small. Δ_i was calculated as the difference between AIC_C for a given model and AIC_C for the highest ranked model (i.e. that with the lowest AIC_C) for all candidate models. Models with $\Delta_i < 10$ were considered to have some support, and those with $\Delta_i < 2$ were considered to have strong support, for being the 'best models', i.e. those having the highest probability to be closest to reality (Burnham & Anderson 2002). Finally, model averaging was applied for all models qualifying as 'adequate' and relative variable importance evaluated. Standard errors were calculated as the square-root of the unconditional variance estimator (Burnham & Anderson 2002, Greaves *et al.* 2006).

To assess the predictive power of the achieved models, a set of three criteria describing model fit (calibration and refinement) and discriminant power was calculated: R^2_N, AUC (area under the receiver operating characteristic curve), which evaluates discrimination (Hanley 1982), and CCR (overall correct classification rate) for discriminative power (Fielding & Bell 1997).

2.2.4 Model transferability and generality

Habitat preferences of a species can vary spatially and temporally (e.g. Whittingham *et al.* 2007). Poor model generality can lead to reduced spatial transferability of models and misleading management decisions (Gray *et al.* 2009). To test the spatial transferability of our results, we developed habitat suitability maps for both study areas (Austin 2002). Of the models containing only those variables with complete coverage for the study area (i.e. excluding variables such as vegetation height, which were collected only at sampling points), that with the lowest AIC_C was selected. In the GIS, grid themes were created describing the value of the considered variables for every grid cell for both study areas. The logistic regression equation for the referring model was then applied to each grid cell, and via a classifying process, areas of the same occurrence probability were ranked equally. Different thresholds distinguishing between suitable and unsuitable habitat were tested, a widely used, but arbitrary level of $p = 0.5$ (e.g. Manel *et al.* 2001), and a threshold of $p = 0.22$ based on prevalence of the presences in the dataset (Liu *et al.* 2005). To externally validate the model on a spatial scale, we assessed the extent to which nest-sites in the NE Kazakhstan study area were situated within areas predicted as 'suitable' by the model from the central Kazakhstan study area used for prediction.

2.3 Spatial analysis of grazing patterns

Because previous work suggested a considerable influence of livestock grazing in habitat selection (Watson *et al.* 2006), we analysed grazing patterns of domestic livestock with a comparatively simple spatial approach to complement the rather mechanistic habitat modelling approach. Whereas horses are very mobile in the study areas and roam over distances of more than 100 km, cattle and sheep herds are now almost exclusively kept on steppe pastures immediately surrounding human settlements. The cattle and sheep of every household in the settlements are collected by shepherds in the early morning, driven radially out of the villages in different herds for grazing and herded back every evening. To quantify the spatial extent of diurnal domestic livestock movements and grazing patterns, GPS data loggers were attached to four cattle in two different villages of the Korgalzhyn study area using specially designed neck collars in May and June 2007. The loggers were programmed to fix the animals' position every 2 min from 6:00 until 18:00 h. These point data were downloaded and processed in the GIS. To estimate grazing intensity, the villages were buffered with concentric bands of 500 m width and the number of logger fixes falling into these distance categories was calculated, corrected for the area of each band. We assumed that the time spent in every distance band, and thus the number of fixes logged to the GPS per band, reflected grazing intensity. As the animals are kept in relatively tight herds all day long, the position of the tagged animal was considered representative of the whole herd. Maximum vegetation height was measured around two villages in the Korgalzhyn study area along eight 5-km transects radiating out at these villages in 45° sectors. Two sets of measurements were made at points along the transects (each 500 m apart), in May and in June 2007.

3. Results

3.1 Breeding habitat and nest-site selection

At the landscape scale (breeding habitat selection), 16 variables were significant predictors of colony distribution in univariate binary logistic regression models ($p < 0.05$). A total of 61 multivariate models qualifying as 'adequate' were obtained. After the model selection process, five models remained with $\Delta_i < 10$ (Table 2a). The weights of the first three models summed to 0.96.

There was a single 'best' model (no other models had $\Delta_i < 2$), which revealed increasing probability of colony occurrence with decreasing distance to settlements and rivers, and decreasing vegetation height (Figure 1). Occurrence probability fell to < 0.1 just 5.4 km away from settlements and 8.5 km away from rivers, and in areas with vegetation taller than 8 cm. The model correctly classified 98.6 % of data points; overall model performance was excellent (R^2_N = 0.916, AUC = 0.995). Model averaging identified three variables with very high weights (Table 2b). The selection of colony sites in proximity to rivers was not an artefact of settlements being situated closer to rivers, as the spatial distribution of villages in the Korgalzhyn study area did not significantly differ from random points with respect to their distance to the nearest river (Wilcoxon rank sum test, $p = 0.176$, $n = 54$).

At the colony scale, eight variables explained significant variation in nest distribution in univariate binary logistic regression models. Seven adequate multivariate models were obtained. After the model selection process, two models remained with $\Delta_i < 10$, their weights summing up to 0.99, although the second model had $\Delta_i > 2$, suggesting only a single 'best' model (Table 3a). This model predicted maximum probability of nest presence at around 10 % cover of animal dung and around 50 % cover of bare soil. Nest occurrence probability decreased quickly with

Table 2. Modelling results at the landscape scale: (a) overview of all models with $\Delta_i < 10$; (b) averaged regression coefficients β with associated standard errors (SE) and relative variable importance $w_+(j)$ for all models considered in model averaging. For variable abbreviations, see Table 1.

(a) Model	AIC_C	Δ_i	w_i
vegH.mod + dist.riv + dist.sett	36.441	0.000	0.679
cov.art + cov.art (sqr) + cov.gras.tot + cov.gras.tot (sqr) + dist.wat + dung.tot	38.474	2.033	0.246
cov.art + cov.art (sqr) + vegH.mod + dist.riv + dist.wat	42.363	5.921	0.035
vegH.mod + dist.riv + dist.wat + dung.tot	43.013	6.572	0.025
cov.stip + dist.riv + dist.sett	46.281	9.840	0.005

(b) Variable	Averaged β	SE	$w_+(j)$
Intercept	4.5861	12.1077	1.000
dist.riv	−0.0003	6.82E-08	0.749
vegH.mod	−0.0977	0.0025	0.744
dist.sett	−0.0009	2.19E-07	0.688
dist.wat	−0.0018	5.98E-07	0.311
cov.art	0.2540	0.0099	0.285
cov.art (sqr)	−0.0033	0.0211	0.285
dung.tot	0.4337	0.0601	0.277
cov.gras.tot	−0.2402	0.0118	0.246
cov.gras.tot (sqr)	0.0004	2.51E-07	0.246
cov.stip	−0.2413	0.0003	0.007
cov.veg	0.1690	0.0388	< 0.001
cov.veg (sqr)	−0.0023	1.94E-11	< 0.001
cov.herb	−0.1136	5.38E-08	< 0.001

Table 3. Modelling results at the colony scale: (a) overview of all models with $\Delta < 10$; (b) averaged regression coefficients with associated standard errors (SE) and relative variable importance $w_+(j)$ for all models considered in model averaging.

(a) Model	AIC_C	Δ_i	w_i
cov.dung + cov.dung (sqr) + cov.veg + cov.veg (sqr) + dist.nest	215.811	0.000	0.899
cov.dung + cov.dung (sqr) + cov.veg + cov.veg (sqr) + vegH.max + dist.nest	220.227	4.416	0.099

(b) Variable	Averaged β	SE	$w_+(j)$
Intercept	−2.5592	3.3102	1.000
dist.nest	−0.0076	8.57E-06	1.000
cov.dung	0.6825	0.1465	0.998
cov.dung (sqr)	−0.0439	0.0010	0.998
cov.veg	0.1202	0.0058	0.998
cov.veg (sqr)	−0.0013	5.81E-07	0.998
vegH.max	−0.0118	5.72E-06	0.101
cov.grass	−0.0328	4.27E-06	< 0.001

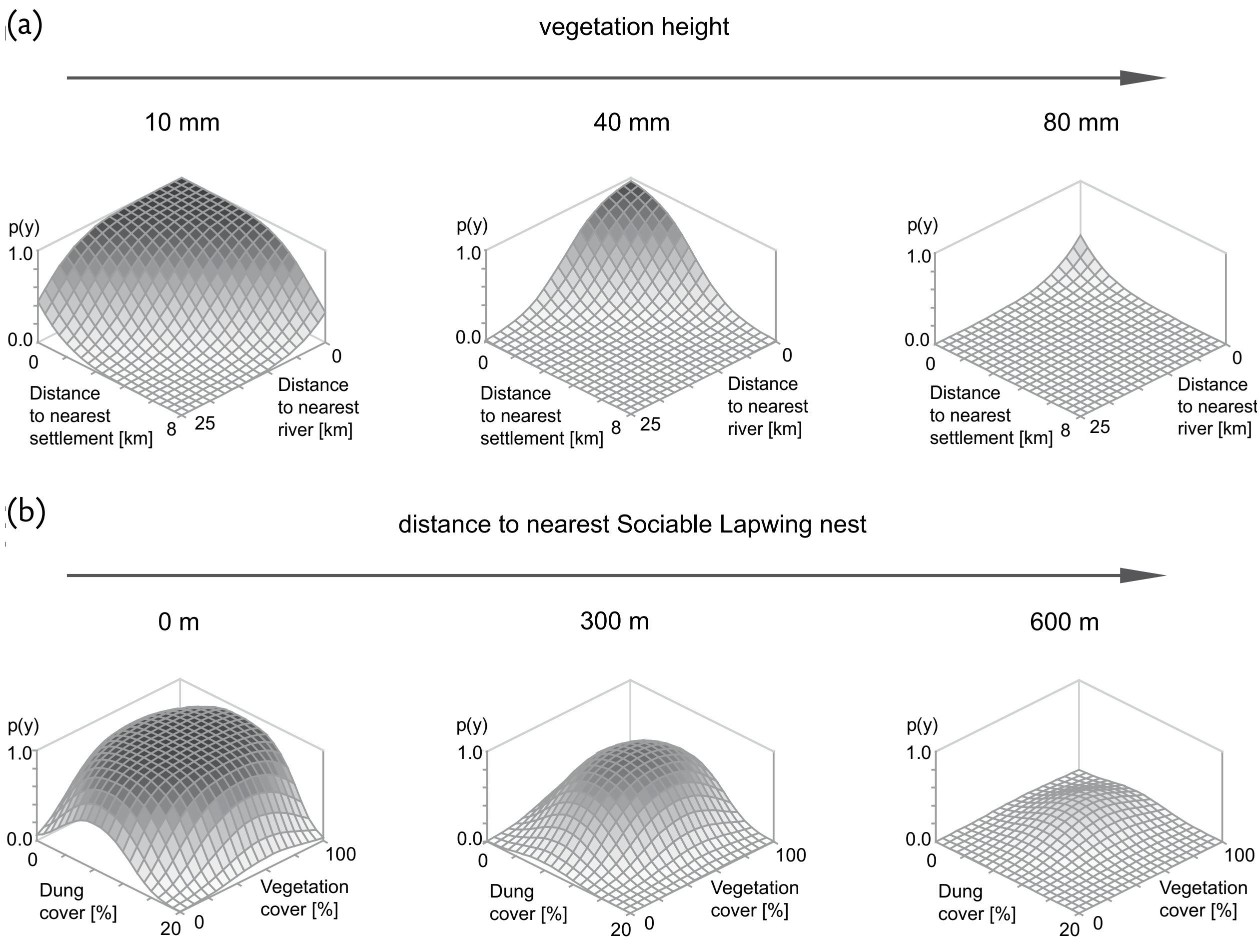


Figure 1. Visualisation of the habitat models with lowest AIC_C ('best models') at landscape (a, above) and colony (b, below) scales. Occurrence probability p is plotted against two variables on the x- and y-axes; diagrams represent different stages of a third variable.

increasing distance to neighbouring breeding pairs, as expected for a colonial species (Figure 1). The model correctly classified 89.5% of the data points, and overall model performance was good (R^2_N = 0.596, AUC = 0.924). Removing the variable 'distance to nearest nest' reduced model fit considerably (R^2_N = 0.344, AUC = 0.820), but the model still explained a high proportion of variation, suggesting a high influence of the cover of bare soil and dung in nest-site selection. Model averaging resulted in three variables (both linear and quadratic terms for each) with very high weights, and one with considerably less weight (Table 3b).

3.2 Spatial prediction and model generality

The model with the lowest Δ_i that included only variables available over the entire area of the study regions contained distance to nearest settlement and distance to nearest river as significant predictors. With AIC_C = 49.8 and Δ_i = 13.4 it was less good than the overall best model, but overall model performance was still very good (R^2_N = 0.812, AUC = 0.979, CCR = 0.964). Applying this modelled to a prediction of apparently suitable habitat distributed patchily across both study areas (Figure 2). Mean area of a predicted suitable habitat patch in the Korgalzhyn region was 4 586 ha (± 397.4 SE, range 458 – 9 639, n = 37). The mean distance between neighbouring patches of suitable habitat was 4.72 km (± 0.78 SE, range 0.1 – 24.1 km). The proportion of habitat predicated as suitable in the Korgalzhyn study region was 6.6% applying a threshold of p = 0.5, and 8.0% using the prevalence approach with p = 0.22.

Spatial generality was good with 74.0% of all nest-sites found in the Pavlodar region in 2007 (n = 146) situated in areas predicted as suitable by the model developed in the Korgalzhyn area (threshold: p = 0.5). Patch occupancy was, however, low, with only 26.7% of all patches predicted as suitable being occupied by breeding Sociable Lapwings in 2007.

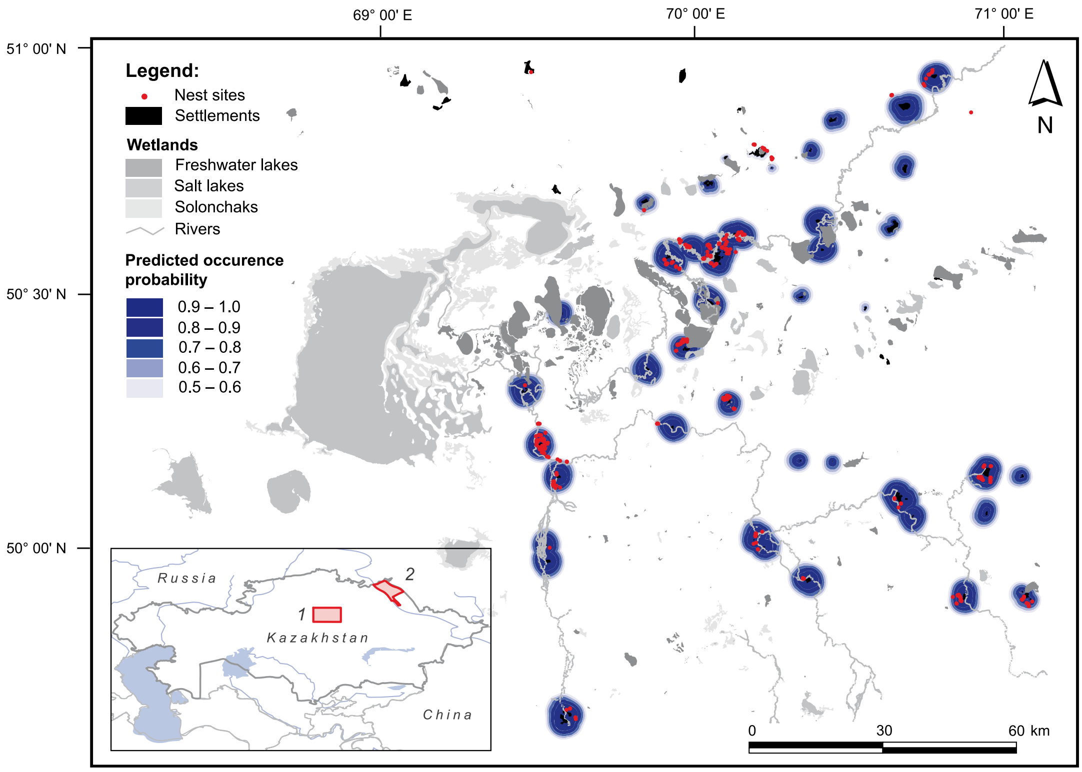


Figure 2. Habitat suitability map for the Korgalzhyn study area. The depth of blue shading indicates differences in occurrence probability. All nest-sites for the years 2004, 2005, 2007 and 2008 are plotted. Inset: Geographical position of the Korgalzhyn (No. 1) and Pavlodar (No. 2) study areas in Kazakhstan.

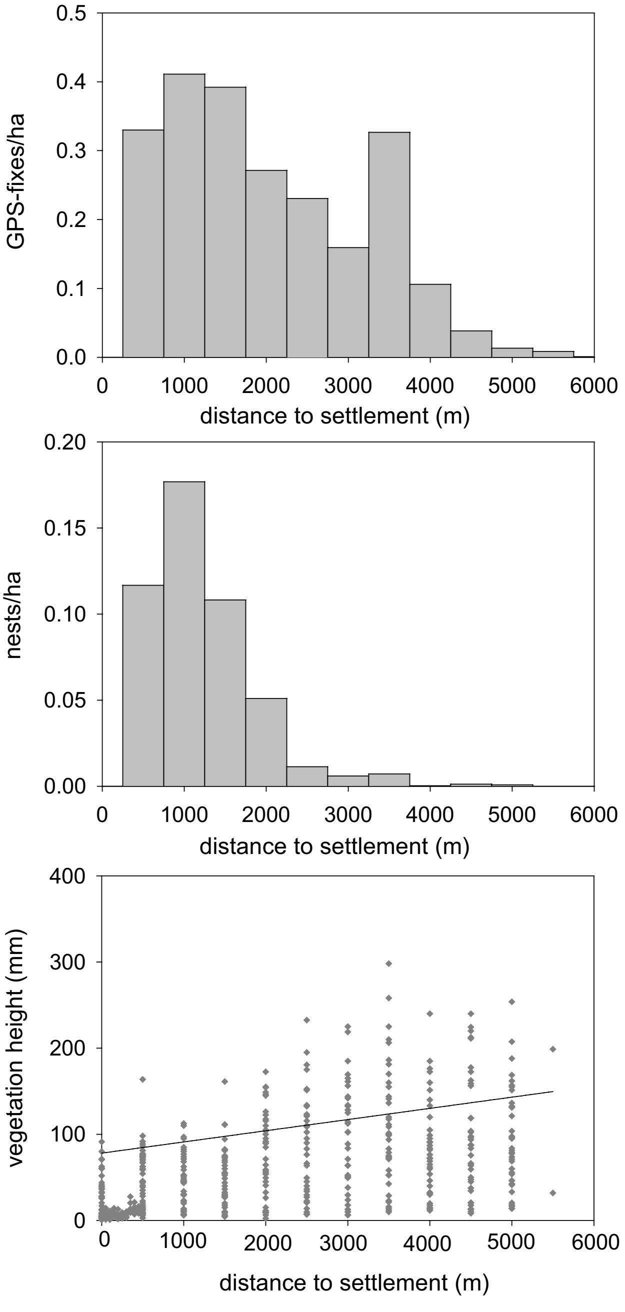


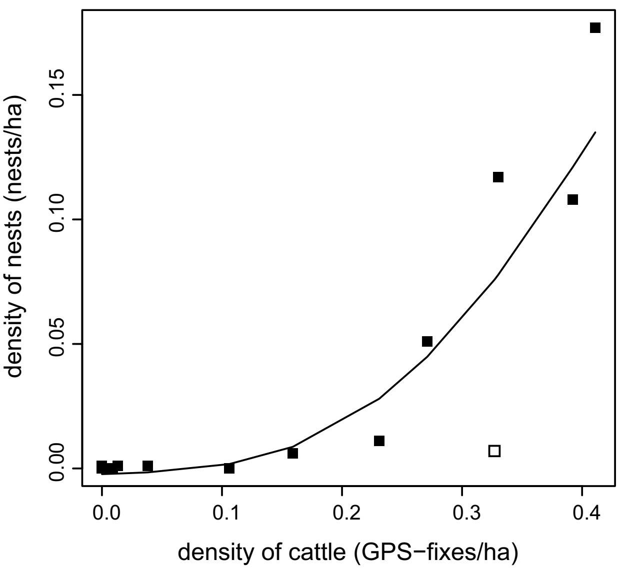
Figure 3 (↑) Grazing intensity of cattle (n = 4 976 GPS-fixes), Sociable Lapwing nest density (n = 673 nests, years 2004 – 2008) and vegetation height around settlements. All density estimates are corrected for distance band area. Vegetation height increased with increasing distance from the nearest settlement (Generalised Linear Model (GLM) including month and site as fixed factors, $X^2_{478} = 93{,}22$, $p < 0.001$).

Figure 4 (→). Relationship between cattle grazing intensity and Sociable Lapwing nest-site location (n = 673 nests, years 2004 – 2008). The line shows a spline smoothing function (df = 3). The outlier (open square) is the result of a water hole approximately 4 km from one village, where cattle spent much time drinking.

3.3 Spatial grazing patterns and Sociable Lapwing nest-site selection

The mean maximum daily distance covered by four cattle tracked with GPS-loggers in the Korgalzhyn study area was 4 330 m (± 419 SE, range 2 100 – 8 300 m, n = 19 track-days with 4 076 GPS-fixes). Cattle always moved radially away from the villages during the day and returned along the same route. Grazing pressure decreased with increasing distance from the settlements with the exception of the 3 000 – 3 500-m band, which had a higher than expected density of GPS fixes because this is where cattle went to drink (Figure 3). Vegetation height increased linearly with increasing distance to the settlements (Figure 3), although variation was high. Mean vegetation height per distance band was negatively correlated with cattle density (Spearman's $r = -0.72$, $p < 0.05$, n = 11 bands).

Most nest-sites were very close to villages, with a mean distance to the nearest village edge of 1 164 m (± 36.0 SE, range 10 – 6 830 m, n = 637 nests in 2004 – 2008). Of all nests, 89 % were situated closer than 2 000 m to the nearest settlement, and thus in the areas with the highest grazer intensity (Figure 3). The density of Sociable Lapwing nests per distance band was strongly positively associated with cattle density per distance band (Figure 4), the relationship suggesting a threshold in grazing intensity needed to create suitable habitat for the Sociable Lapwing.



4. Discussion

4.1 Breeding habitat and nest-site selection

Breeding habitat selection of the Sociable Lapwing at a landscape scale appears to be driven by two key factors: proximity to rivers and the presence of grazing animals. The first of these might result from the species' migration strategy: birds often migrate along rivers, which serve as orientation strips and water supply in the monotonous steppe landscape (J. Kamp, R. D. Sheldon pers. obs. from colour-ringed and satellite-tagged birds 2006, 2007). Suitable habitat might thus simply be selected more often closer to rivers, because these areas are encountered first. Alternatively, the preference of breeding sites close to water might be driven by the fact that both adults and chicks visit water bodies to drink during hot days (Dolgushin 1962, J. Kamp, R. D. Sheldon pers. obs.).

All other variables with high weights in models pointed to the influence of grazing in habitat selection. Vegetation height and the density of dung piles were strongly correlated with the density of grazing livestock in the Central Kazakhstan study area, and the preference for habitat close to human settlements is linked to the fact that livestock grazing is currently concentrated there. The remaining variables with considerable weight (preference for a high wormwood *Artemisia spp.* cover and avoidance of a high cover of grassy plants and feather grass *Stipa spp.*) mirror vegetation characteristics of heavily grazed steppe communities: Grasses, especially feather grass, are positively selected by grazing livestock, as they are palatable, leading to an increased abundance and cover of the unpalatable *Artemisia* and other woody plants with increasing grazing pressure (Bock *et al.* 1984, Baker & Guthery 1990, Yunusbaev *et al.* 2003).

The selection of colony sites near rivers was not an artefact of settlements being situated closer to rivers. However, cattle numbers might be higher in settlements situated at river shores (due to the unlimited availability of drinking water). This might lead to higher grazing pressure and thus more suitable habitat available closer to rivers.

In the Korgalzhyn study area we covered many areas previously known as breeding sites of Sociable Lapwings, which were often situated close to human habitation. This represents a source of possible bias when evaluating the influence of settlements on Sociable Lapwing distribution. However, we consider a systematic influence on the modelling results as very unlikely, as more than 1 000 km of additional survey transects were covered in randomly chosen habitats when gathering distribution data for the models.

Within the colonies, the most influential variable in nest-site selection was distance to nearest nest, as to be expected for a colonial species. Removing this variable again suggested selection of more heavily grazed areas for nest placement, as both the cover of dung and the cover of bare ground generally increase with increasing grazing pressure by domestic livestock (Bock *et al.* 1984, Yunusbaev *et al.* 2003). These results from the modelling approach were supported by the spatial analysis of grazing patterns, which revealed a strong relationship between grazing intensity and Sociable Lapwing nest density, and confirmed the suggestions of Watson *et al.* (2006) on nest-site selection.

The excellent transferability of a landscape model containing only the distance to rivers and settlements as covariates suggests that the availability of water and short swards around settlements are key factors in habitat selection across the whole breeding range. However, the number of patches occupied in the test area was very low. This indicates the absence of important covariates in the model used for prediction (e.g. vegetation height), suggesting that not all habitat predicted as 'suitable' is indeed suitable for Sociable Lapwing breeding. Low patch occupancy rates might also indicate that there is much more habitat available than currently used, particularly at this north-eastern limit of the species' range.

4.2 Reasons for synanthropy

Breeding Sociable Lapwings are now almost entirely confined to short steppe swards close to human settlements. This type of habitat has been described previously in relation to this species, but only since 1990 (Khrokov 1996, Berezovikov *et al.* 1998, Eichhorn & Khrokov 2002, Bragin 2005, Watson *et al.* 2006). Sociable Lapwings were previously described as breeding in other habitats, such as pristine fescue-feather grass steppe and semi-desert (Volchanetskii 1937, Ryabov 1974, Khrokov 1977, Shevchenko 1999) as well as the shores of saltpans vegetated with short swards of halophytes ('solonchaks', Kuchin and Chekcheev 1987, Gordienko 1991, Shevchenko *et al.* 1993), but these seem to be virtually unused now. Arable fields have only ever been used rarely for breeding (Solomatin 1997, Karyakin & Koslov 1999). This current synanthropic relationship might be considered as a form of commensalism with domestic livestock. High dung densities are known to increase invertebrate abundance (Atkinson *et al.* 2004), and the pronounced preference for areas with a high density of dung might indicate the use of an improved food base on strongly grazed pastures. A high proportion of Sociable Lapwing nests (68 % of 168 nests found in 2006, Korgalzhyn study area) were actually built in piles of cattle or horse dung. Sociable Lapwings choosing dung piles for nesting might profit from a camouflaging effect of dry dung, or insulation from the ground, which is often still frozen during the start of incubation in April. Away from the immediate vicinity of villages, the steppe is now largely ungrazed after the collapse of wild ungulate populations, such as wild ass *Equus hemionus* and Saiga antelope (the latter declining by 95 % in 1994 – 2002, Milner-Gulland *et al.* 2001), and because of the reduced mobility of livestock owners compared with Soviet times.

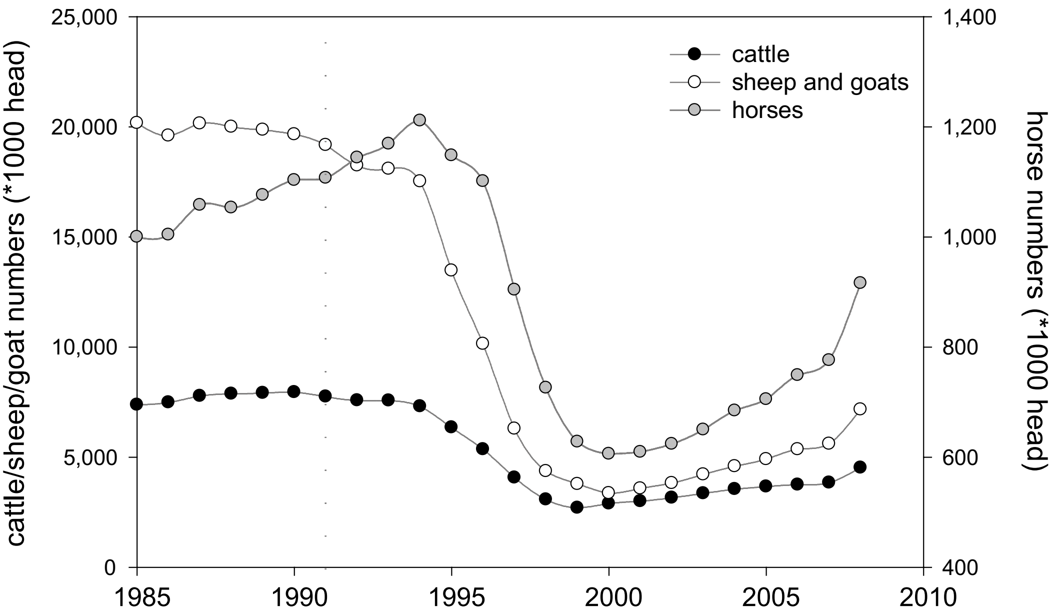


Figure 5. Trends in livestock numbers for the districts ('oblasts') of Kazakhstan situated in the steppe belt ($n = 8$), between 1985 and 2008 (Kazakhstan State Statistics Agency 2008). The Soviet Union collapsed in 1989 and Kazakhstan gained independence in 1991.

4.3 Land use change and population development: implications for conservation

Although the reasons for a population decline in Sociable Lapwing have not yet been clarified, there are suggestions that the population trend has matched land use changes on the breeding grounds. During Soviet times (c. 1930 until 1991), most livestock were owned by large state companies, and extremely low fuel prices and the widespread availability of machinery enabled farmers to distribute their livestock widely across the steppe pastures (Robinson *et al.* 2003, Milner-Gulland *et al.* 2006). After the collapse of the Soviet Union in 1991, livestock numbers crashed both in Russia and Kazakhstan due to a withdrawal of state subsidies and the use of animals as currency in times of economic hardship (Suleimanov & Oram 2000, Robinson & Milner-Gulland 2003). Since 2000, this negative trend has been reversed (Figure 5).

Large-scale wheat farming was introduced in Kazakhstan during the 'Virgin Lands Campaign' 1953 – 60, when 25.4 million ha were ploughed in the steppe belt. After 1991, huge areas of arable land fell fallow (De Beurs & Henebry 2004). The area used for crop-growing was reduced by nearly 40 % during the 1990s (Suleimanov and Oram 2000). This trend has been reversed since around 2000: in the eight districts of Kazakhstan situated in the steppe belt, the area sown for cereal crops steadily increased by an average of 31 % (± 6.3 SE, range – 8.5 to 45.4 %) during the period 2000 – 2008.

Population trends of the Sociable Lapwing seem to be strongly correlated with the changing availability of short-grazed habitat. The highest breeding numbers were reached around 1900, when post-breeding flocks of 8 000 – 10 000 birds were observed (Plotnikov 1898) and the species was a 'common breeder' in Eastern Kazakhstan and Russia (Finsch 1879). The range contraction and severe decline observed in the 1930s and 1950s (Dolgushin 1962, Ryabov 1974) coincide with agricultural intensification. Further declines during the Soviet period might have been linked to intensification in farming and an increased livestock mobility leading to lower grazing pressure in steppe habitat. A strong decline of Sociable Lapwing numbers after 1991 has been linked repeatedly to the cessation of grazing in many areas following the collapse of livestock numbers (Tomkovich & Lebedeva 2004).

After 2000, however, livestock concentration increased the suitable breeding area for Sociable Lapwing at least in Central and Northern Kazakhstan and are mirrored by a positive population trend. Numbers in our Korgalzhyn study area increased by 48 % between 2005 and 2007 (R. D. Sheldon, J. Kamp, M. A. Koshkin unpubl. data), in the Pavlodar study area by approximately 23 % between 1991 and 2007 (Solomatin 1997, J. Kamp, M. A. Koshkin pers. obs.), and also in other regions of Kazakhstan, e. g. the Naurzum region, N Kazakhstan, between 2000 and 2008 (Eichhorn & Khrokov 2002, Bragin 2005).

However, two recent developments mean that the current situation might change soon. First, there is likely to be an increase in the reclamation of fallow land and agricultural intensification of steppe land. A doubling of grain prices since 1999 (FAOSTAT 2008) and a record harvest in 2007 (Kazakhstan State Statistics Agency 2008) have enabled farmers to buy expertise and equipment and return to large-scale farming in many parts of the northern steppes. Cereal yield has increased by 41.5 % since 2000 (Kazakhstan State Statistics Agency 2008). World food demand has been predicted to double by 2050 (Tilman *et al.* 2002), and the production of bioethanol is rapidly increasing (IAE 2007), so increasing quantities of cereals will be demanded on the world markets. Kazakhstan opened its first bioethanol plant in 2008, with a capacity of 350 000 tons of cereal products, and a rapid increase of this business is expected (Biohim 2008).

Secondly, there are likely to be significant changes in livestock management. A stable economic growth in Kazakhstan since 2000 has led to a steady improvement of living standards, accompanied by a tendency for rural migration to the cities. It thus seems likely that the current livestock management system characterized by village-based herding of self-sustaining communities might soon give way to more intensive systems with animals kept concentrated day and night in large stables, and an increasing tendency to give up small-scale animal husbandry. Both processes would result in a decrease of suitable habitat for the Sociable Lapwing and other steppe species such as Black-winged Pratincole *Glareola nordmanni* and White-winged Lark *Melanocorypha leucoptera*.

Whereas habitat availability and low breeding success seem currently not to be limiting factors in Sociable Lapwing populations (R. D. Sheldon, J. Kamp, M. A. Koshkin unpubl. data), future developments in steppe land use, especially changes in grazing patterns and expansion and intensification of agriculture, should be monitored closely. A continued monitoring of Sociable Lapwing numbers and productivity across the distribution range would be highly desirable. Important stopover sites have been discovered recently, but distribution, habitat use and threats at the migration routes as well as on the wintering grounds are largely unknown. More insight could lead to better conservation in the whole life cycle of this charismatic, yet much depleted, species.

Acknowledgements

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CHAPTER 5

Kamp J, Koshkin MA , Sheldon RD (2009)

Population size, breeding performance and habitat selection of the Black-winged Pratincole *Glareola nordmanni*

Bird Conservation International 19: 149 – 163

Author contributions: JK developed the research ideas, collected the data, conducted the analysis and wrote the paper. MAK and RDS provided additional data on nest sites from earlier years.

Summary

The population of the Black-winged Pratincole *Glareola nordmanni* has declined significantly during the course of the 20th century, resulting in a classification as 'Near Threatened' and 'Endangered' in the Global and European Red Data Books, respectively. Reasons for the decline are largely unknown due to a lack of information on the breeding ecology of the species. We studied breeding performance and habitat use of the Black-winged Pratincole in two areas in Kazakhstan and evaluated a new world population estimate. Colony size ranged from two to 180 pairs and differed significantly between the study areas. Mean breeding success was 1.30 ± 0.16 (mean ± SE) fledged chicks per breeding pair in Central Kazakhstan, and 0.59 ± 0.13 (mean ± SE) fledged chicks per breeding pair in NE Kazakhstan. Habitat types preferred were intensively grazed natural steppe, abandoned and fallow fields, shores of freshwater and brackish lakes and solonchaks (salt pans). Factors influencing habitat selection were quantified the first time for this species: the probability of occurrence of breeding colonies was highest near human settlements, within 3 km of open water and where sward heights were low or intermediate, indicating a reliance on heavy grazing and water. Using data from six surveys across the whole breeding range, we calculated a new world population estimate of 76 000 – 95 000 breeding pairs, which is substantially higher than previous estimates. We discuss colony size, habitat use and population trends in the light of changing landscape conditions in the steppe zone and suggest an increase in habitat available to Black-winged Pratincole due to an increase in the area of fallow fields and a change in grazing regimes since the collapse of the Soviet Union in 1991.

1. Introduction

The Black-winged Pratincole *Glareola nordmanni* is a breeding endemic of the Eurasian steppe zone. Its breeding distribution is largely restricted to Southern Russia and Kazakhstan, with single pairs or small colonies in Ukraine, Belarus, Armenia, Azerbaijan, Romania and Hungary (Belik & Lebedeva 2004; Figure 1). The species winters in southern Africa, mainly in Botswana and the Republic of South Africa. Due to a historical population decline lasting at least until 2000, the species has recently been globally uplisted to 'Near Threatened' (Birdlife International 2007), with an estimated population of 29 000 – 45 000 mature individuals. In the European Red Data Book, the Black-winged Pratincole is listed as 'Endangered' (Birdlife International 2004) due to dramatic declines in European Russia and the almost complete loss of the Ukrainian population (Belik *et al.* 2000, Belik 2004, Belik & Lebedeva 2004).

Around 1850, Black-winged Pratincole population size was significantly larger than today, and post-breeding flocks even in the smaller European part of the breeding range numbered hundreds of thousands of birds (Kessler 1851). Declines have been reported from all over the breeding range since 1910, and the European breeding population declined by 40 – 60% after the collapse of the Soviet Union (Belik 2004, Belik & Lebedeva 2004). A contraction at the western part of the range was observed, leading to a possible extinction of Black-winged Pratincole in Ukraine. In central southern Russia, the results of large scale surveys point to a slight to pronounced increase in numbers since the beginning of the 1990s (Karyakin & Koslov 1999, Korshikov 2002). Trends in Kazakhstan, the stronghold of the species, have never been quantified, but numbers appear to have increased slightly between 1998 and 2007 (A.V. Koshkin pers. comm. 2007, A. O. Solomatin pers. comm. 2007).

Factors behind population declines are poorly studied. Belik & Lebedeva (2004) presented an overview, including the following main factors in the breeding areas:

i) ploughing of steppe (more than 25 million ha in Kazakhstan) resulting in habitat loss and low breeding success in colonies on arable fields,

ii) trampling of clutches and chicks due to lower mobility and stronger concentration of livestock compared to previous times,

iii) higher predation rates by increasing numbers of corvids, and

iv) climate change with increasing frequencies of extreme weather (e.g. hailstorms) and droughts.

Information on habitat use of the Black-winged Pratincole is largely anecdotal or based on low sample sizes. The availability of freshwater for drinking, short vegetation, and the presence of livestock were mentioned by a number of authors (Koshelev 1983, Samorodov 1986, Karyakin and Koslov 1999, Korshikov 2002, Belik 2004, Belik & Lebedeva 2004). In European Russia, where large areas of natural steppe are ploughed up, Black-winged Pratincoles are known to nest in significant numbers both on arable (Moseikin *et al.* 2004) and on fallow and abandoned (hereafter referred to as fallow only) fields (Moseikin *et al.* 2004, L. Malovichko pers. comm. 2007). Livestock grazing seems to be important for the species, because it creates short swards available for nesting and might improve food supply, as coprophagous insects are attracted by dung.

As published information on population numbers, habitat use and breeding success is limited, the Single Species Action Plan for the species (Belik & Lebedeva 2004, see also BirdLife International 2007) stresses an urgent need for research on population ecology and dynamics. Here we present quantitative data on Black-winged Pratincole abundance, breeding performance and habitat use from two study areas in Kazakhstan. Our results might serve as a first step to implement broader, conservation-orientated research.

2. Methods

2.1 Study areas

Fieldwork was carried out during the breeding season 2006 in proximity to Lake Tengiz, 120 km SW of Astana, Kazakhstan (Figure 1; cf. also Schielzeth *et al.* 2008). The village of Korgalzhyn constitutes the largest settlement. The study area covered approximately 200 km x 150 km (30 000 km²) and stretched between 49°40′ – 50°55′ N and 68°38′ – 70°59′ E. In 2007, approximately 12 000 km² were surveyed in Pavlodar region in NE Kazakhstan within a study area situated along the lower Irtysh river between the settlement Akku (= Lebyazhe, c. 51°28′ N / 77°46′ E) and the Russian border at c. 53°47′ N / 75°03′ E (Figure 1).

The Korgalzhyn study area (Central Kazakhstan) is dominated by flat short-grass steppe and (mostly fallow) cereal fields in the north and hilly semi desert in the south. The area is characterised by many fresh and saline lakes (the latter known as solonchaks), the largest being the saline Lake Tengiz with an area of approximately 1 380 km². It is a highly important breeding and stop-over site for waterbirds (Schielzeth *et al.* 2008).

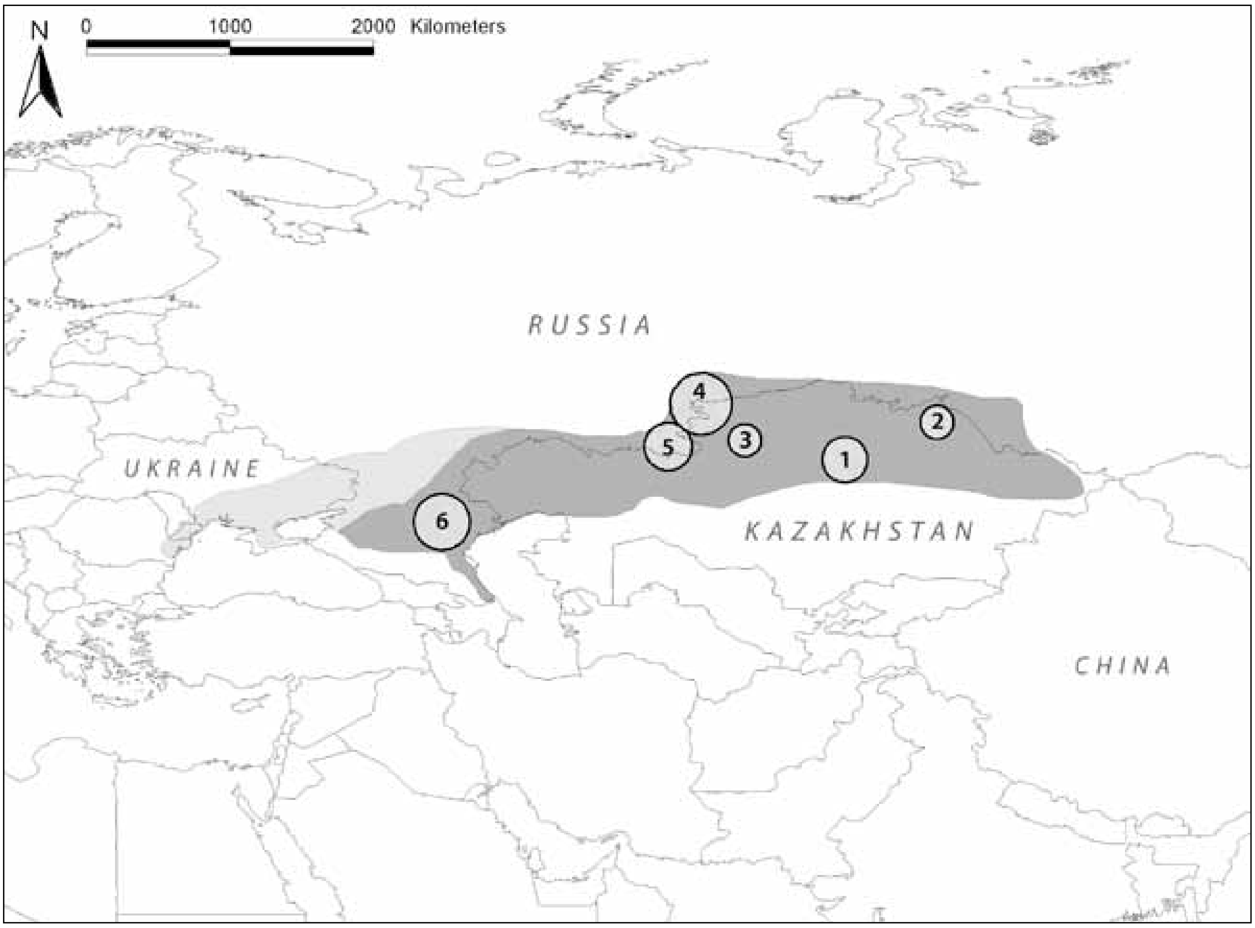

Figure 1. Location of the Korgalzhyn and Lower Irtysh study areas (nos. 1 – 2) and areas of further surveys considered for the population estimate (nos. 3 – 6) within Kazakhstan and Russia. Numbers correspond to those in Table 2. Circle size is proportional to the area of the region surveyed. The dark grey area shows the current breeding distribution of Black-winged Pratincole, across the light grey area, the species is considered extinct.

The Lower Irtysh study area is dominated by the Irtysh River. The river has never been straightened, and the floodplain (16 km wide) is inundated for 16 – 43 days per year (A. O. Solomatin pers. comm. 2007), chiefly in May. Oxbow lakes, extensive reeds and willow thickets are interspersed with late-mown hay meadows. The adjacent landscape on both sides of the river is characterised by herb-rich tall-grass steppe and small birch forests.

In both study areas, the character of steppe vegetation is strongly influenced by domestic grazing with livestock concentrated around human settlements. This leads to an unequal grazing pressure resulting in dense, tall stands of fescue *Festuca sulcata* and feather grass *Stipa lessingiana* where grazing intensity is low, and wormwood *Artemisia spp.* dominated short swards where livestock is concentrated.

2.2 Sampling design and data recording

The Korgalzhyn study area was surveyed for Black-winged Pratincoles from the end of April to the end of July 2006, the Lower Irtysh study area from the end of April to the end of July 2007. We surveyed all previously known breeding sites of Black-winged Pratincole, on which information was available from local databases and expert communication (Schielzeth *et al.* 2008, V. V. Khrokov 2007, in litt.), as well as all wetland sites similar to habitat used in previous years (freshwater lakes with open shores, solonchaks). Furthermore, we surveyed large areas of fallow fields as well as pristine steppe. Due to the huge size of the study area, this was done from a vehicle. We partly stopped at vantage points and surveyed the area using a telescope, partly watched out for pratincoles driving transects with low speed (c. 20 – 30 km hr^{-1}). The total length of survey transects driven across the areas was approximately 1 200 km in 2006 and 700 km in 2007. Habitat obviously unsuitable for breeding pratincoles (such as birch forest in the Lower Irtysh area, reeds and open water) was not surveyed. Black-winged Pratincoles often hunt in flight near breeding colonies and are thus very obvious over large distances, hence car-based surveys are regarded as a suitable method. Using telescopes, flying pratincoles can be identified at even larger distances, in good light conditions up to several kilometres.

We estimate that combining the approaches described above we were able to cover approximately 75 % and 80 % of the area suitable for breeding pratincoles. The remainder comprises mainly complexes of contiguous wheat fields, which often cover several thousand hectares, and are inaccessible to normal vehicles. Due to the rather cursory nature of the car-based surveys, all numbers presented here should be considered as minimum figures.

When a colony was located, the number of adults was recorded, combining repeated counts of flying and sitting / incubating birds. Most colonies were subsequently visited every 3 – 10 days until chicks fledged. As the sex ratio within the colonies was observed to be mostly even (sexes can be separated by plumage differences and size when seen together and birds remain paired during incubation), the maximum number of birds present in a colony during the nest initiation period was divided by two and the resulting number used as an approximation to the number of breeding pairs. A colony was defined when either incubating birds or chicks were seen, or nests were found.

To estimate breeding success, colonies were visited when the chicks had just fledged and still did not fly well enough to cover large distances. Recently fledged juveniles tend to gather in dense post-breeding flocks at the colony site, accompanied by alert adults flying around them in a loose group. Overall breeding success per pair was calculated by dividing the number of fledged chicks by the number of estimated breeding pairs. This could be done only for some colonies, because in other colonies juveniles had already started to disperse from the colony site.

To analyse differences in habitat selection between the study areas, main terrestrial habitat types were defined using our own classification. Factors influencing breeding habitat selection were studied on the landscape scale in the Korgalzhyn study area in 2006 using a presence-absence habitat modelling approach. The sample unit was the single breeding colony. A colony was defined as an aggregation of breeding pairs at least 3 km apart from the next breeding incidence to avoid strong autocorrelation. Habitat parameters to be examined for an influence on Black-winged Pratincole breeding habitat selection were chosen on the basis of published information suggesting that especially the availability of water and low vegetation influence habitat selection (Belik 2004). Parameters recorded included 'maximum vegetation height' and 'distance to nearest permanent water feature'. As our own observations in the study areas from previous years suggested that the presence of livestock is an important factor as well, the variable 'distance to nearest settlement' was additionally included. This has been proved a strong correlate of both dung densities and livestock abundance in the Korgalzhyn region (Spearman's $r > 0.9$; J. K. 2006 unpubl. data). Within the colonies, all parameters were measured at a nest site in the centre of the colony. This was considered representative for the whole colony. These colony points representing 'presence' were compared with points randomly selected across one third of the study area (containing the whole range of habitats and covering the whole latitudinal gradient). Random points were automatically defined on a map using a random point generator in ArcView 3.2a (Jenness 2005). Effective sample size was limited by the scattered distribution of the colonies throughout the study area. Thirty-five colonies were available for variable sampling and 109 random points were generated to collect absence data, thus prevalence was higher than the minimum of 20 % suggested by Bonn & Schröder (2001).

Vegetation height (mm) was recorded in the field using a simple folding rule, distance values were calculated in ArcView 3.2a. Vegetation height was recorded in the period 25 May – 16 June 2006. Since vegetation growth within the recording period would limit comparability of single presence / absence points and model quality, vegetation height measurements were repeated at 60 points chosen randomly out of the predetermined presences and absences once in Korgalzhyn region. Vegetation height did not differ significantly between measurements taken on 21 May and 5 June 2006 (Wilcoxon test: $Z = -1.3, p = 0.175, n = 67$).

2.3 Data analysis

The proportion of every habitat type within the study area was estimated from Landsat 7 ETM+ scenes representing habitat availability, and breeding habitat selectivity was assessed using the Jacobs preference index (Jacobs 1974).

To analyse habitat selection, binary logistic regression was used (Hosmer & Lemeshow 2000). A univariate analysis was conducted first for all variables separately to test for correlation with presence or absence as suggested by Hosmer & Lemeshow (2000) and in order to avoid spurious inclusion of variables in a multivariate model. We tested correlations between predictors to avoid multicollinearity (Graham 2003), but since correlations were generally weak (all $r_S < 0.5$) we included all predictors in a full model. We used a stepwise backward procedure (critical p-value $p_{out} = 0.10$ for variable removal, likelihood-ratio test) for model simplification. All models were fitted in SPSS 15.0. Before processing variables in multivariate models, the shape of the environmental relationship was determined, i. e. the pattern of each variable's response to environmental factors. This has often been neglected, but is a crucial factor when using statistical models to predict species abundance and distribution (Austin 2002). Relationships can be either sigmoid (with positive or negative characteristic) or unimodal ('bell-shaped' or 'bowl-shaped'). Whether a relationship was sigmoid or unimodal was tested by assessing which variant provided the best fit to the data by the level of significance. If both relationships were significant, the one with the stronger response (according to Nagelkerke's R^2, Strauss & Biedermann 2006) was chosen.

To assess the predictive power of the final models, several measures of model quality were calculated:

i) Nagelkerke's R^2, which describes model calibration and refinement (Nagelkerke 1991),

ii) AUC (area under the receiver operating characteristic, ROC), which describes discrimination (Hanley 1982, McNeil & Hanley 1984), and

iii) Cohen's Kappa, which describes discriminative power prevalence-independent (Manel *et al.* 2001).

All models were internally validated using bootstrapping (Manly 2001) with 300 iterations. Measures for model quality and bootstraps were calculated using the SPlus 6.1 statistical package.

We calculated a new world population estimate using the large-scale breeding densities derived from our study and from other recent surveys across the entire distribution range of the species. A minimum and maximum density value ($\hat{D}$) for each survey (equation 1) was calculated according to the minimum and maximum number of breeding pairs (n_{pairs}) found in area A. Minimum numbers refer to counted pairs, maximum numbers refer to estimated maximum numbers.

$$\frac{\hat{D}=n_{pairs}}{A} \qquad (1)$$

Subsequently, the mean minimum and maximum density per area were averaged for all surveys (equation 2).

$$\hat{D}_{mean} = \frac{\sum_{k=1}^{n} \hat{D}_k}{n_{surveys}} \qquad (2)$$

To achieve a new estimate for the world population ($N_{pairs.tot}$), we multiplied this density by the range of the current distribution of the Black-winged Pratincole (A_{tot}), which was estimated rather conservatively at 1 922 311 km² (GIS data) after reviewing the relevant literature (J. K. 2007 unpubl. data) and considering the species as extinct in Ukraine (BirdLife International 2004):

$$N_{pairs.tot} = \hat{D}_{mean} * A_{tot}. \qquad (3)$$

We consider this way of extrapolation to be sound, because

i) large scale population densities from six studies were fairly similar (cf. Table 2),

ii) the area covered by all surveys combined was large (200 000 km² or approximately 10 % of the species' distribution area) and

iii) the study areas were distributed across the whole range of the species and included marginal populations.

3. Results

3.1 Local population numbers and densities

In total, 1 207 breeding pairs in 35 colonies were recorded throughout the Korgalzhyn study area and a total of 627 breeding pairs in 41 colonies throughout the Lower Irtysh study area. Since only about 75 % and 80 % respectively of the areas could be covered, the population size was estimated to reach c. 1 500 pairs in the Korgalzhyn area and c. 785 pairs in the Lower Irtysh area. This equals a large scale population density of 3.8 (survey count) to 4.7 (estimate) breeding pairs / 100 km² for the Korgalzhyn area and 5.2 to 6.4 breeding pairs per 100 km² for the Lower Irtysh area.

3.2 Colony size

Colony size was significantly smaller in the Lower Irtysh area with 1 – 70 breeding pairs per colony (15.3 ± 19.1, mean ± SD) compared to the Korgalzhyn study area with 2 – 180 pairs per colony (34.5 ± 37.7, mean ± SD) (Mann-Whitney U-Test: Z_{76} = −2.9, p = 0.004). Most colonies consisted of 1 – 10 pairs in both areas, while colonies with more than 100 pairs (n = 2) were found exclusively in the Korgalzhyn area (Figure 2).

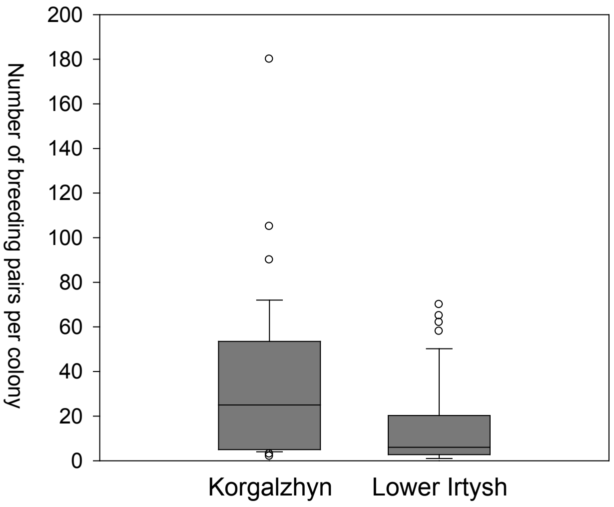

Figure 2. Comparison of Black-winged Pratincole colony size (number of breeding pairs per colony) in both study areas.

3.3 Breeding phenology

First (already paired) birds were seen on 28 April 2006 in the Korgalzhyn area and on 7 May 2007 in the Lower Irtysh area. First nests were found on 4 May and 14 May respectively. As they mostly contained incomplete clutches of one or two eggs, they were considered as fresh. Hence, these dates are probably close to the overall start of the egg-laying period. There was no first hatching date recorded for Korgalzhyn region. In the Lower Irtysh region, first chicks hatched on 6 June 2007 (n = 12 nests). First fledged chicks were observed on 1 July 2006 in Korgalzhyn, and on 5 July 2007 in the Lower Irtysh study area. Clutch size was 3.41 ± 0.51 (mean ± SD, n = 12 nests) in the Lower Irtysh region.

3.4 Breeding success

Breeding success was 1.30 ± 0.16 (mean ± SE, range 0.82 – 1.78, n = 6 colonies) fledged juveniles per pair in the Korgalzhyn study area and 0.59 ± 0.13 fledged juveniles per pair (mean ± SE, range 0.00 – 2.33, n = 20 colonies) in the Lower Irtysh region. Breeding success was significantly lower in colonies of the Lower Irtysh study area compared to that of the Korgalzhyn area (t = 3.8, df = 24, p = 0.005), but since the two sites were sampled in different years, site and year effects cannot be separated. Around several empty scrapes, droppings of foxes and hedgehogs were found, suggesting that predation by these species was an important cause for clutch loss. Trampling by livestock was observed only once, but there was evidence from eggshell remains that sheep flocks in the Lower Irtysh study area trampled further nests in 2007.

3.5 Habitat use and selection

In the Korgalzhyn study area, the majority of colonies were located at muddy shores of freshwater and slightly saline lakes (23 % of all colonies) and dried-out solonchaks (salt pans) with a dense cover of *Salicornia spp.* (49 %). In the Lower Irtysh area, most colonies were found on intensively grazed swards on natural steppe (39 %) and fallow arable fields (24 %) dominated either by Wormwood *Artemisia sp.* or Fescue *Festuca sp.* Breeding on recently sown arable fields and burnt steppe was recorded in the Lower Irtysh region only. Intensively grazed steppe, shores of freshwater and brackish lakes, and solonchaks were the preferred habitat types in both areas (Figure 3).

There was a stronger preference for wetland habitats in the Korgalzhyn region, whereas in the Lower Irtysh study area fallow and grassland habitat were slightly preferred. Grazing livestock was present at all colonies (usually throughout the breeding season, but in some cases at the beginning of the breeding season only).

Maximum vegetation height, distance to nearest village and distance to nearest permanent water feature all differed significantly between colonies and random points (likelihood-ratio test, $p < 0.001$, Table 1), suggesting that colonies in the Korgalzhyn area in 2006 were not randomly sited with respect to these three variables. In a second step, we fitted a multivariate model including all three predictors.

Diagnostic statistics showed that the model fitted the data well and internal validation did not significantly reduce model quality (Nagelkerke's $R^2 = 0.906$, AUC = 0.988, Cohen's $\kappa = 0.926$, bootstrapped model). 97.2 % of all presence- and absence-points were classified correctly. Occurrence probability decreased with increasing distance to settlements (including cattle brigades) and permanent water features. Maximum vegetation height strongly influenced distribution patterns as well, with an occurrence probability peak (i.e. habitat optimum) reached at $h \approx 50$ mm (Figure 4).

3.6 World population

Based on large-scale breeding density estimates from this study and recent literature data (Table 2, Figure 1), we extrapolated a new world population estimate of 76 416 – 95 143 breeding pairs, approximated to 76 000 – 95 000 breeding pairs.

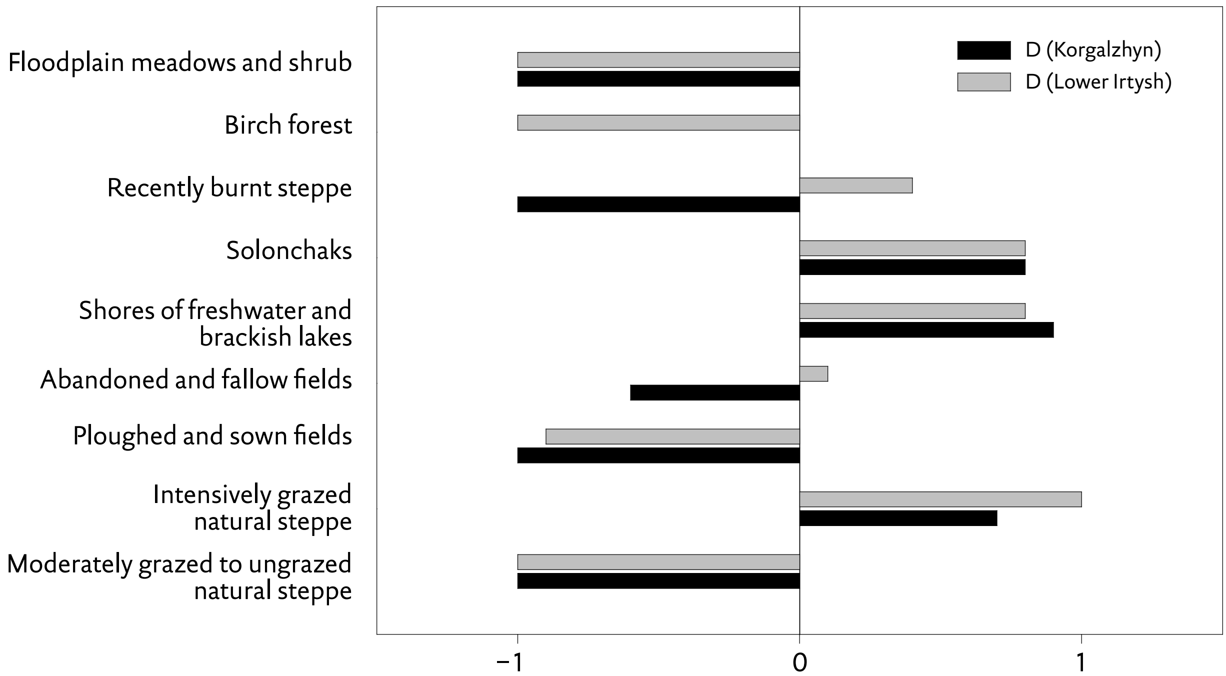

Figure 3. Comparison of breeding habitat use of Black-winged Pratincole in both study areas described by the Jacobs preference index D. Values < 0 indicate an avoidance of the habitat type referred to (−1: complete avoidance), those > 0 indicate a preference for the habitat type referred to.

Table 1. Variables examined with logistic regression for an influence in Black-winged Pratincole habitat selection. *p* values, measures of model fit and response direction for all univariate logistic regression models are given.

Variable	p	R^2_N	AUC	Cohen's κ	Response shape
maximum vegetation height	<0.00001	0.653	0.960	0.770	unimodal
distance to nearest permanent water feature	<0.00001	0.635	0.928	0.701	sigmoid negative
distance to nearest settlement	<0.00001	0.452	0.872	0.632	sigmoid negative

Table 2. Overview of recent large scale surveys for Black-winged Pratincole. 'pairs min.' refers to minimum number of breeding pairs counted / estimated, 'pairs max.' means estimated maximum numbers.

	Area	Source	Survey year	Area size (km²)	Pairs min	Pairs max	Density min (BP/100km²)	Density max (BP/100km²)
1	Korgalzhyn, Central Kazakhstan	Kamp *et al.* (this paper)	2006	31,800	1,207	1,500	3.80	4.72
2	Lower Irtysh, NE Kazakhstan	Kamp *et al.* (this paper)	2007	12,000	627	785	5.23	6.54
3	Naurzum reserve, W Kazakhstan	Bragin 2004	2004	12,000	429	586	3.58	4.88
4	Chelyabinskaya oblast', S Central Russia	Karyakin and Koslov 1999	1999	87,000	2,000	4,000	2.30	4.60
5	Orenburgskaya oblast', S Central Russia	Korshikov 2002	1999	40,000	2,500	2,500	6.25	6.25
6	Stavropolskii Krai, SW European Russia	L. Malovichko in litt. 2007	2006	66,500	1,800	1,800	2.71	2.71

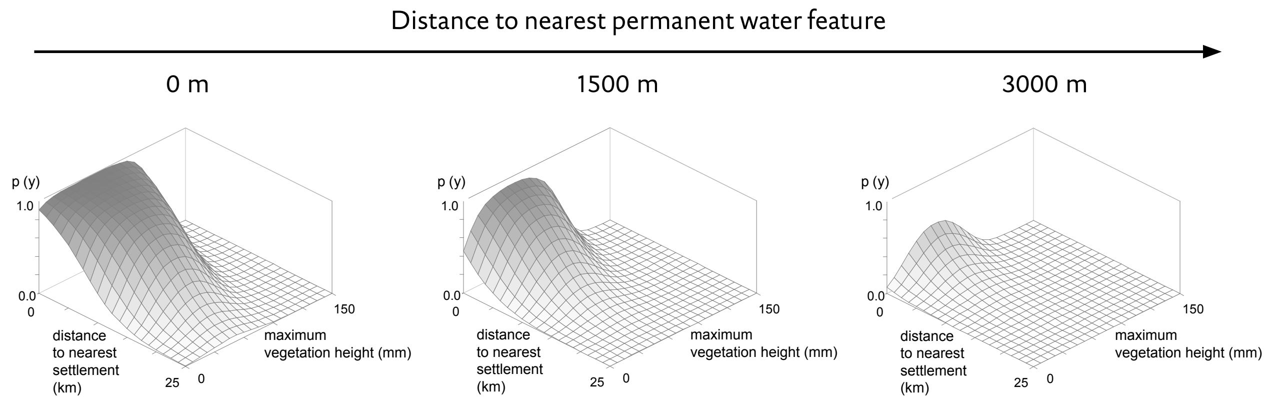

Figure 4. Multivariate habitat model including all three recorded habitat variables. Occurrence probability (*p*) is plotted against distance to nearest settlement and maximum vegetation height. Diagrams represent different stages of the distance to water features.

4. Discussion

4.1 Colony size and breeding performance

The colony sizes ascertained for the study areas considered here are fairly similar to the range cited in the literature. Across the southern Russian breeding grounds, most colonies hold 3–20 pairs, with larger ones up to 150 pairs (Koshelev 1983, Davygora *et al.* 1992, Karyakin & Koslov 1999, Korshikov 2002, Belik 2004, L. Malovichko in litt. 2007). The largest colonies found in recent years held 500 pairs (Stavropol region 2006, L. Malovichko in litt. 2007) and 1 200 pairs (Orenburg province, Korshikov 2002). For Kazakhstan, Dolgushin (1962) mentions colonies of 'few, dozens, hundreds and sometimes thousands of pairs'. During the last 10 years no colonies larger than 100 pairs have been reported, except one colony of 600 pairs on the shore of the Caspian Sea near Atyrau in 2003 (S. Erokhov in litt. 2008).

There is no published information on the level of productivity that is required to maintain population stability in pratincoles. Lysenko (1980) found 50 % nest loss and 30 % chick loss caused by livestock trampling for breeding colonies in Ukraine. For the Collared Pratincole *Glareola pratincola*, Calvo (1994) found high hatching rates in marshland colonies (88 % of clutches hatched), but lower rates on farmland (29 % hatched). Belik & Lebedeva (2004) and Belik (2004) suggest both nest failure and chick mortality to reach 60 – 100 % in Black-winged Pratincole annually, but this is based on a study of 'colonial waders' in Central Kazakhstan and does not necessarily concern Black-winged Pratincole (Elkin 1981). Productivity of 1.30 chicks per pair in 2006 (Central Kazakhstan) exceeds that required by well-studied species, such as Northern Lapwing *Vanellus vanellus* (where 0.72 – 0.84 chicks per female need to be produced annually to maintain population stability, Catchpole *et al.* 1999). Productivity of 0.59 chicks per pair as observed in 2007 in NE Kazakhstan is probably below this level. It is not clear why the level of productivity differs between the two study areas or years, but it may be linked to a difference in predation rates due to a shortage of voles in 2007 leading to an increase in predation by small carnivores (R. D. S. 2007 unpubl. data). Moseikin *et al.* (2004) found 100 % clutch loss after agricultural operations on arable land with four nesting colonies comprising a total of 610 pairs. This seems not to be an exception, as in our Lower Irtysh study area a colony of 30 pairs was extirpated by harrowing just after colony initiation. However, birds failing early in the breeding period could move to other sites and initiate replacement clutches.

4.2 Habitat use and selection

As habitat selection is a hierarchical process of behavioural responses, neither proximate nor ultimate factors can be determined by simply studying current bird distributions (Jones 2001). The results presented can provide only hints to this process. Our analysis quantified the high importance of livestock grazing and the availability of water in habitat selection, and suggests a preference for a distinct vegetation height, at least for the Central Kazakhstan population.

Suitable habitats were selected more often close to water, which might be due to the availability of drinking water for adults (Dolgushin 1962). Occurrence probability approached zero already 3 km from permanent water features in the Central Kazakhstan study area suggesting Black-winged Pratincoles in steppe areas are dependent on the proximity to wetlands.

Obviously, an important proximate factor in habitat selection of Black-winged Pratincole is the presence and density of grazing livestock, suggested by the fact that short-grazed areas close to human settlements were preferred. However, solonchaks with *Salicornia* cover and muddy (salt and freshwater) lake shores produce a suitable vegetation height for natural reasons (hydrological conditions, salt dynamics). These areas are frequented by livestock mainly for resting and drinking, which leads to high dung densities. Dung might increase food abundance (coprophagous insects around dung piles and Diptera attracted to grazers), as birds have been seen pecking dung beetles from fresh and decaying dung piles (J. K. pers. obs., Atkinson *et al.* 2004). As clutches are often embedded in dung piles, other hypotheses include a possible heating effect of decaying dung, use of dung piles as orientation marks to facilitate recovery of own clutches in a colony environment, and, most likely, a camouflage effect of dung piles on embedded clutches.

4.3 Population numbers

We estimated the world population to approximately 76 000 – 95 000 breeding pairs, equalling 152 000 – 190 000 mature individuals. This estimate is significantly higher than the latest estimate of 29 000 – 45 000 mature individuals (BirdLife International 2007), which was largely based on 'best guess' for the Asian part of the distribution area (V. V. Khrokov pers. comm. 2006). The new population estimate is supported by a recent count from a single site on the wintering grounds: 76 500 birds were present at Vaal Dam, South Africa, in 2006 (University of Cape Town 2006). In 1991, an even larger flock of 250 000 to 800 000 birds was observed in Orange Free State, South Africa (du Plessis 1995). A post-breeding flock of 20 000 birds at Manych wetlands, SW Russia in September 2006 (M. A. K. 2006 unpubl. data) indicates higher numbers in European Russia.

Pratincoles are known to exhibit a sporadic distribution pattern, i.e. the distribution and size of colonies vary noticeably between years (Belik 2004). As we used data from different areas and different years, our population estimate might be biased upwards, assuming that birds from a study area surveyed early abandoned it and then moved to another that was surveyed subsequently. However, given the background of the recent high counts on passage and in the wintering areas, and because all surveyed areas are quite distant from each other, we regard it as unlikely that the new estimate is strongly biased due to this reason.

4.4 Population trends in the light of changing steppe land use and habitat availability

Land use changed significantly across the Eurasian steppe belt within the last 100 years. The steppes of Ukraine and European Russia had been ploughed almost completely by 1900, whereas in Asian Russia and Kazakhstan, the proportion of arable land was negligible until the 1950s and grazing by domestic animals was the most widespread type of land use. After the Second World War, the 'Virgin Lands Campaign' of the Soviet government heavily affected the steppe ecosystem: Between 1953 and 1961, 41.7 million ha (25.4 million ha in Kazakhstan) of steppe were ploughed, mainly for wheat cultivation (Wein 1983).

Livestock numbers were high in Kazakhstan until the 1930s (an estimated 150 million livestock units [LU] in 1930; Robinson & Milner-Gulland 2003), but crashed then due to the rigorous enforcement of the Soviet collectivisation policy and the resulting emigration of over one million nomads (around 14 % of the population) to China and Mongolia (only 25 million LU left by 1935). From 1950 to 1991, livestock numbers increased steadily, reaching 100 million LU at the end of the Virgin Lands Campaign, and were back to the level of the 1930s by 1990 (Robinson & Milner-Gulland 2003).

After the collapse of the Soviet Union in 1991, institutional changes led to the end of the state crop subsidy system. This resulted in large-scale abandonment of arable fields across Kazakhstan (De Beurs & Henebry 2004). The area sown for crops in Kazakhstan was reduced by 38 % through the mid-1990s (Suleimenov & Oram 2000). In the Korgalzhyn study area, even 60 – 80 % of all formerly agriculturally used area fell fallow between 1991 and 1998 (own analysis from Landsat 7 ETM+ imagery). Livestock numbers both in Russia and Kazakhstan crashed after the collapse of the Soviet Union due to the withdrawal of state support and the use of animals as currency. In all Russian steppe regions combined, total livestock numbers (cattle, horses, sheep and goats) decreased by 49 % (GosKomStat 2001). In Kazakhstan, the political and economical changes affected livestock numbers as well, resulting in a decline of 58 % in cattle and 75 % in sheep and goats from 1990 to 1999 (Suleimenov & Oram 2000, Robinson & Milner-Gulland 2003). These figures are fairly representative for our study areas, as outlined by Lenk (2001). Since about 2002, livestock numbers have been increasing again by approximately 10 % in our study areas (J. K. 2008, unpubl. data).

Our study revealed that Black-winged Pratincole is largely dependent on the presence of large grazers. Although precise figures on population trends are lacking, there is evidence that population development (overview in Belik 2004, Belik & Lebedeva 2004) is at least partly a function of habitat availability: Declines occurring from the end of the 19th century in Ukraine and European Russia have been associated with the increase in ploughed area and a loss of grazed steppe. A further rapid decrease recorded in the 1950s was probably related to massive habitat loss during steppe ploughing under the Virgin Lands Campaign. A stable and locally positive trend in numbers during the Soviet period until the 1990s might have been linked to then increasing livestock numbers, as well as the sudden decline by 40 – 60 % (Belik 2004) in the 1990s going along with a crash in livestock numbers, the latter causing former pastures to be overgrown with dense, weedy vegetation.

There is evidence that the large decline of pratincoles described for the second half of the 20th century has halted now in larger parts of the range east of the Ukraine. L. Malovichko (in litt. 2007, Table 2) counted 1 800 breeding pairs in an area in European Russia in 2006, where only 100 – 200 were estimated in 2002 (Belik 2004). Karyakin and Koslov (1999) noticed an increase in numbers in southern Russia after a pronounced decline during the Soviet era. Korshikov (2002) revealed higher numbers compared to Soviet times numbers in a south Russian stronghold, and there is evidence that in central and north-eastern Kazakhstan the number of pratincoles has increased by 20 – 30 % between 1998 and 2007 (A. V. Koshkin pers. comm. 2007, A. O. Solomatin pers. comm. 2007).

This increase coincides with the massive increase of fallow and abandoned land described above, and indeed, 25 % of all breeding pairs in NE Kazakhstan (this study), and 40 % of the breeding pairs found by L. Malovichko (in litt. 2007; Table 2) in European Russia nested on fallow and abandoned land.

However, former arable areas are only suitable habitats for Black-winged Pratincoles during the first years after abandonment, as the vegetation of mainly weedy species tends to get too tall and dense if not grazed constantly, so pratincoles might not benefit from these areas in the long term.

Changing grazing patterns might have influenced pratincole numbers as well. Whereas during the Soviet era total livestock numbers were an order of magnitude higher than today, overall grazing pressure was probably less. The animals were driven further away from settlements and state farms, in order to avoid overgrazing and simply because arable fields started mostly right at the edges of villages (Robinson *et al.* 2003).

Since privatisation of the livestock sector in the 1990s, people tend to keep the herds in close vicinity of settlements for logistical reasons. The migration of stock to summer pastures across the steppe belt has ceased due to a lack of transport facilities. In localized areas, this leads to much higher grazing pressure than in Soviet times, turning former tall grassland, fallow hay and wheat fields into short-grazed swards. These areas are used by a large proportion of the pratincoles in our study areas (see Results).

Apart from habitat availability, there might by other threats to the species (see Introduction). Farming intensity is still high in some areas of Russia and across Ukraine, so arable fields might function as 'ecological traps', i.e. attract pratincoles to breed, but weaken the population due to low breeding success (Moseikin *et al.* 2004). However, it is not clear to what extent arable fields attract pratincoles for breeding as these are difficult to survey. In both our study areas they were used by a minor proportion of the population.

Trampling of clutches at the strongly grazed areas around settlements might be a problem, and sheep flocks driven at speed through colonies can cause significant clutch loss (J. K. 2007 unpubl. data; see also Watson et al. 2006 for the ecologically close Sociable Lapwing *Vanellus gregarius*). However, the comparatively high fledging rates revealed in our study indicate that trampling might be less of an issue than expected.

4.5 Implications for conservation

As described above, the decline of Black-winged Pratincole numbers was apparently not as dramatic as suggested by Belik & Lebedeva (2004), and the world population seems to be substantially larger than previously thought. Habitat availability seems to have increased during recent years. However, there is no doubt that especially in the European parts of the range the species has decreased significantly in numbers. A range contraction and increasing isolation of breeding areas has occurred, and the species might have recently become extinct in Ukraine.

As the Black-winged Pratincole remains understudied, we suggest a focus on research at the breeding grounds on

i) the current distribution and numbers at the edges of the species' range (SW Russia, Ukraine, E Kazakhstan),

ii) past and likely future land use and habitat changes across both the breeding and wintering range and their effect on population development

iii) the level of productivity and reasons for clutch loss as well as chick mortality in different habitats (especially whether arable fields function as ecological sinks).

To reduce the risk of trampling by livestock, an approach that takes into consideration rural communities is much needed. Talking to shepherds and suggesting they avoid the colony areas might help to increase breeding success. If trampling is an issue, fencing colonies might be an option. In Russia, Sociable Lapwing clutches on arable land hatched successfully, when conservationists informed farmers and solicited the exclusion of the colony area from harrowing (Morozov 2005).

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CHAPTER 6

Conclusions and Outlook

Changes in agricultural land-use on the Eurasian steppes, stretching from Ukraine to the Western Siberian Altai Mountains, have been extreme since the dissolution of the Soviet Union in 1991. In this thesis, I quantify agricultural change in Kazakhstan for the decades 1991 – 2000 and 2000 – 2010 and reveal a pattern of agricultural abandonment and destocking in the 1990s, but a trend towards reclamation of abandoned land and a recovery in livestock numbers in the past decade. Based on governmental statistics and interviews with land managers, I forecast an ongoing reclamation and intensification of arable land in the years to come, along with a trend of increases in numbers, but also a redistribution of currently concentrated livestock.

I set out to examine the impact of these changes on a key species group in the region, steppe birds. Collecting large-scale bird density data and distribution information previously unavailable, and relating these to habitat features influenced by land-use, I could show that there is an overall strong response in steppe bird populations on different spatial scales to both the intensity of arable farming and grazing patterns of domestic ungulates (chapter 1).

Distribution and abundance of steppe birds seems mainly to be governed by small-scale differences in vegetation height, plant cover (i.e. the availability of bare ground) and animal dung abundance, suggesting a co-evolution with the native grazers that shaped vegetation communities of the Eurasian steppes before they were hunted to extinction or severely depleted by man. Grazing of livestock replacing the original vast herds of wild ungulates seems to be beneficial to the persistence of steppe birds, for example certain species of lark (chapter 3). In the absence of native wild ungulates, domestic ungulates might even be indispensible as certain steppe waders such as Sociable Lapwing (chapter 4) and Black-winged Pratincole (chapter 5) would not breed before a threshold of grazing intensity (quantified by my research for the first time) is reached. Apart from vegetation features shaped by grazers, the availability of dung seems crucial for the latter species as clutches were placed directly into piles of cattle dung, possibly for camouflaging or insulating reasons. Grazing patterns seem to impact on steppe bird distributions at different scales, from the landscape-scale (lark abundance along a gradient of grazing intensity, chapter 3) to meso-scales (nest-site selection in heavily grazed areas with high dung densities by Sociable Lapwings and Black-winged Pratincoles, chapters 4 and 5). Changes in grazing management seem to have impacted on a behavioural level as well, leading for example to pronounced synanthropy in Sociable Lapwings not observed in Soviet times (chapter 4). Also, grazing intensity seems to play an important role in niche segregation of closely related species, as demonstrated here for the lark family (chapter 3).

Abandonment of farmland led to secondary steppe succession, and abandoned fields represent a habitat of major importance to some steppe species reaching extremely high densities in these habitats (chapter 1). In contrast, arable fields used for wheat cultivation have proven overall poor habitats, hosting few species in very low densities. Reclamation of arable land for farming thus has and will have major implications for the status and persistence of steppe birds.

The current situation for birds (and biodiversity beyond birds) in the steppes of Kazakhstan, and thus the largest and most important part of the Eurasian steppes, might seem rather positive. There is an overall low human population density, and various intensities and varying patterns in agricultural land-use shape the landscape such that there is 'something for everyone'. However, the future might not look that bright. Pressure on the vast grasslands will undoubtedly increase in future years, as the human population of Kazakhstan is rising fast, mostly in rural areas (Kazakhstan State Statistics Agency 2011), and the government follows a strategy of unlimited economic growth with annual rates of 5 – 8% (CIA 2011). Processes impacting ecosystem services and biodiversity negatively are likely to increase in the future: due to increasing consumption levels (and to a lesser extent due to increasing human population), world food and energy demand are predicted to increase massively over the next decades (Tilman *et al.* 2002). Kazakhstan is one of the world's leading exporters of oil, gas and mineral resources and food, and substantial profits from these industries are increasingly being reinvested in agriculture. High grain prices make cereal agricultural a profitable business at the moment, and will probably continue to do so. Kazakhstan, aided by development agencies and banks from early-industrialised countries, has recently launched a strategy to reclaim more land, modernise the agricultural sector, diversify the crop portfolio and move towards industrialised agriculture as found over much of Western Europe (Kazakh Ministry of Agriculture 2008). Tendencies to abandon more or less traditional livestock breeding methods, resulting in the concentration of cattle in stables year round and the provision of hay silage grown on steppe soils instead of herding flocks on the steppe are observed in parts of Kazakhstan (Kazmarketing 2009).

Ambitious, energy-consuming development and infrastructure projects such as the translocation of the country's capital city to the heart of the steppes, transcontinental oil pipelines and giant road schemes connecting production facilities in China with consumer markets in Europe (Gizitdinov 2006) will potentially have big impacts on steppe ecosystems.

Conservation monitoring and action will thus be required in the future, probably more than currently. In my thesis, I provide the baseline data to guide decisions in bird conservation, allowing the development of strategies to maximise benefits to biodiversity while not impairing living standards of the human populations. These would ideally comprise:

i) A set-up of monitoring systems for land-use change and biodiversity responses, e.g. via remote sensing applications (Buchanan *et al.* 2008a, Buchanan *et al.* 2008b) and bird and mammal monitoring schemes (e.g. Singh & Milner-Gulland 2011)

ii) A more quantitative approach to protected area selection using algorithms maximising cost-effectiveness and benefits for biodiversity (Rodrigues *et al.* 2004), i.e. improvements to the current opportunistic strategy of Protected Area Selection in Kazakhstan (e.g. Zuther 2009). The Eurasian steppes are among the ecozones with the lowest proportion covered by protected areas (Brooks *et al.* 2004).

iii) Lobbying at the government institutions of Kazakhstan for more wildlife-friendly farming, by measures such as agri-environmental schemes and a biodiversity-friendly adjustment of state subsidies in the arable and livestock sector.

The research presented in this PhD-thesis covers only a tiny proportion of the questions that can be asked and might be answered to better understand landscape-scale processes in the steppes of Eurasia, which have been heavily affected by post-Soviet change.

The mosaic of used and abandoned fields and areas of varying grazing pressure are likely to continue to provide a useful, pseudo-experimental setup for both basic and applied ecological researchers for a number of years. A few examples of potentially rewarding research approaches are:

i) A more detailed evaluation of steppe bird responses to agricultural management throughout the seasons. There is evidence that wheat fields might be of greater importance to some steppe birds after harvest (R. Urazaliev unpublished data, 2010), and this might have implications for survival and productivity of species breeding in adjacent steppe.

ii) An extension of the work described here to other taxonomic groups, e.g. an evaluation how insects, namely the numerically dominant grasshoppers and locusts beyond the 'pest' species were affected by agricultural abandonment and how this translated into bird responses.

iii) Modelling of current and future multi-level ecosystem processes, such as an evaluation to which extent increased wildfire frequency and availability of fresh burns impacted on small mammals and birds, or which other multi-species-group interactions (e.g. domestic livestock grazing – small mammal abundance – burrow-inhabiting bird abundance) were affected by changing grazing patterns.

iv) An assessment of whether Saiga antelope still has an ecosystem-wide impact despite its much depleted population, or whether it is no longer a keystone species, and how this might change along the projected recovery.

v) A rigorous evaluation of concurring conservation strategies summed up in the 'Land-sparing vs. land-sharing' debate (Green *et al.* 2005, Phalan *et al.* 2010, Phalan *et al.* 2011).

Finally, an extension of the work beyond biodiversity seems rewarding, e.g. establishing how other ecosystem services such as carbon sequestration, soil fertility and hydrological regimes are affected by current and future land-use changes. With predicted changes in weather and climatic patterns, an incorporation of climate as well as land-use change into any future research seems imperative. Only integrated, landscape-scale approaches incorporating ecological, but also socio-economic perspectives will be suited to preserve the unique steppe ecosystems of Eurasia for future generations.

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Summaries

Executive summary

In this thesis, I quantify changes in agriculture on the Eurasian steppes that were triggered by the dissolution of the Soviet Union, and evaluate their impact on populations and the ecology of steppe birds in Kazakhstan. I use habitat modelling techniques and socio-economic research to detect patterns in species responses to agricultural change and predict future developments. Data were collected in 2006 – 2010 in three study areas in Kazakhstan.

Agriculture across the Eurasian steppes is characterised by arable farming, mostly for cereal crops, and livestock breeding. Cultivation for arable crops started early in Ukraine and European Russia, and at the end of the 19th century, hardly any steppe was left in pristine condition. In Kazakhstan, significant areas of the steppe grasslands were cultivated as late as the 1950s during the Soviet 'Virgin Lands Campaign'. After the break-up of the Soviet Union, roughly half of the farmland in the steppe zone was abandoned during privatisation of the state farm system. However, economic growth and increasing wheat prices led to widespread reclamation of abandoned farmland from the year 2000 onwards, and currently an increasing intensification and mechanisation of farming practises is observed.

Livestock numbers were rather high in the beginning of the 20th century, but crashed during the collectivisation in the 1930s. They recovered quickly and increased massively during Soviet times, and collapsed during 1993 – 1995 as state subsidies were withdrawn and animals used as currency in times of economic hardship. In most regions of Kazakhstan, livestock numbers recover slowly, but there are areas with no recovery in both Kazakhstan and Southern Russia. Grazing patterns changed from nomadic systems in the beginning of the 20th century, to semi-nomadic approaches in Soviet times and a concentration around settlements after 1991 leading to a very imbalanced grazing pressure across the steppes.

Numbers of native wild ungulates grazing the steppe crashed early due to overhunting, and the only species surviving in significant numbers during the 20th century was the Saiga antelope *Saiga tatarica*. However, poaching for meat and horn (for traditional Chinese medicine) burgeoned in the 1990s leading to a 98 % reduction of the population in 2003, from around a million animals to a mere 30 000.

Overall, population responses of steppe birds to arable change were pronounced. Modelling bird population density on large scales in a representative region in central Kazakhstan along a land-use gradient ranging from pristine steppe to arable fields and heavily grazed pastures (chapter 2), I was able to show that long-abandoned arable fields and ungrazed pristine steppe were the most important habitats for most species. This suggests that due to post-1991 abandonment of arable agriculture, many species have enjoyed a period of significant population growth during the years 1991 – 2000 and later. Livestock concentration effects, leading to high grazing pressure in small areas, are also likely to have benefitted several species of high conservation concern, such as the endemic White-winged Lark *Melanocorypha leucoptera* or the Critically Endangered Sociable Lapwing *Vanellus gregarius*. An analysis of land-use statistics and dedicated socioeconomic surveys among land managers suggest that recent and predicted future trends in agriculture in the steppe zone, particularly the reclamation of abandoned cereal fields and reduced grazing pressure, may cause populations of most species, including a number of biome-restricted species, to decline in the near future. I discuss possible conservation solutions, including improvements in the protected area system and land-sparing options.

Changing grazing patterns, a decline in domestic and wild ungulates, more frequent wildfires and abandonment of arable agriculture led to massive changes in vegetation. To investigate, how

these changes impacted on bird communities on a mesoscale, I assessed niche separation in larks (Alaudidae), which are the dominant bird family across the Eurasian steppe zone (chapter 3). I examined the extent to which the distributions of different species of lark vary along the two main agricultural gradients in the steppe and semi-desert zones of Kazakhstan: the intensity of grazing and the time since abandonment of cereal fields. Vegetation structure and composition varied significantly and non-linearly with time since abandonment, and with varying livestock density. The lark species examined responded in non-linear ways to both these gradients and showed a high degree of niche separation, with Black Lark *Melanocorypha yeltoniensis*, Calandra Lark *Melanocorypha calandra* and Skylark *Alauda arvensis* preferring denser and taller vegetation as found on abandoned arable fields compared to White-winged Lark and Short-toed Lark *Calandrella brachydactyla*, which were found in areas with more open ground and more xerophytic vegetation. Lark populations generally are likely to have benefitted from agricultural abandonment and a decline in livestock numbers over large parts of the steppes and semi-deserts of the former Soviet Union. My data suggest that an assessment of future changes in steppe bird communities based upon projections of changes in the area of gross habitat types (as done in chapter 2) can be improved by a better understanding of the responses of different species to more subtle environmental gradients.

By modelling habitat associations and the distribution of breeding Sociable Lapwings, a Critically Endangered steppe wader (chapter 4), I discovered even further reaching implications of land-use change, in this case leading to a high degree of synanthropy due to changes in livestock grazing patterns. At a landscape scale, breeding colonies were strongly positively associated with villages and rivers. Habitat suitability models had very high predictive power and suggested that only 6.6 – 8.0 % of the 30 000-km^2 study area was potentially suitable for Sociable Lapwings. Models developed to describe the spatial distribution of nests in one region of Kazakhstan in one year predicted well the distribution of nests in another region, suggesting good generality. At a colony scale, nests were most likely to be found in the most heavily grazed areas, with a high cover of animal dung and bare ground. Despite the low density of human settlements in the study area, most Sociable Lapwing nests were < 2 km from a village. There was a strong positive correlation around villages between grazing intensity and the density of Sociable Lapwing nests, with clear evidence of a threshold of grazing density that needs to be reached before birds will breed. These findings are important for developing management solutions to improve the conservation status of this threatened steppe wader.

A very similar strong reliance on domestic grazers was found in the Black-winged Pratincole *Glareola nordmanni*, which has declined significantly during the course of the 20th century, resulting in a classification as 'Near Threatened' and 'Endangered' in the Global and European Red Data Books. Reasons for the decline are largely unknown due to a lack of information on the breeding ecology of the species. I studied breeding performance and habitat use in two areas in Kazakhstan and evaluated a new world population estimate (chapter 5). Colony size ranged from two to 180 pairs and differed significantly between the study areas. Mean breeding success was 1.30 ± 0.16 (mean ± SE) fledged chicks per breeding pair in Central Kazakhstan, and 0.59 ± 0.13 (mean ± SE) fledged chicks per breeding pair in NE Kazakhstan. The probability of occurrence of breeding colonies was highest near human settlements, within 3 km of open water and where sward heights were low or intermediate, indicating a reliance on heavy grazing and water. Using data from six surveys across the whole breeding range, I calculated a new world population estimate of 76 000 – 95 000 breeding pairs, which is substantially higher than previous estimates and has been adopted by BirdLife International. I suggest an increase in habitat available to Black-winged Pratincole due to an increase in the area of fallow fields and a change in grazing regimes since the collapse of the Soviet Union in 1991. In my thesis, I provide the baseline data to guide decisions in bird conservation, allowing the development of strategies to maximise benefits to biodiversity while not impairing living standards of the human populations. I suggest improvements to the monitoring of biodiversity and land-use change as well as reserve selection schemes, and conclude that lobbying at the government institutions of Kazakhstan for more wildlife-friendly farming is necessary. Finally, I suggest further research options and identify gaps.

Zusammenfassung

In der vorliegenden Arbeit quantifiziere ich tiefgreifende Nutzungsänderungen in der Landwirtschaft in den Steppen Eurasiens, die durch den Zerfall der Sowjetunion im Jahre 1991 ausgelöst wurden. Ich untersuche den Einfluss dieser Änderungen auf die charakteristischen Vogelgemeinschaften der Steppen und beschreibe Auswirkungen auf Populationsökologie und Verbreitung. Dabei werte ich tierökologische Daten, die zwischen 2006 und 2010 in drei Untersuchungsgebieten in Kasachstan gewonnen wurden, mit Verfahren der statistischen Modellierung aus und setze sie in Bezug zu sozioökonomischen Forschungsergebnissen, um zukünftige Entwicklungen vorauszusagen.

Die landwirtschaftliche Nutzung der Steppen Eurasiens wird dominiert von Weizenanbau und Viehzucht. In den Steppen Russlands und der Ukraine begann die Kultivierung früh, und schon am Ende des 19. Jahrhunderts war kaum noch naturnahes, ungepflügtes Grasland vorhanden. In Kasachstan wurde der überwiegende Teil der Steppen erst in den 1950er Jahren im Rahmen der sogenannten ‚Neulandkampagne' umgebrochen. Nach der Auflösung der Sowjetunion wurde während der Privatisierung der Staatsbetriebe etwa die Hälfte der Anbaufläche aus ökonomischen und sozialen Gründen aufgegeben. Ab dem Jahr 2000 führte starkes Wirtschaftswachstum und steigenden Weizenpreise auf dem Weltmarkt zu einer erneuten Beackerung vieler dieser aufgegebenen Flächen, und aktuell lässt sich eine zunehmende Intensivierung und Mechanisierung im Getreideanbau beobachten. Die Viehbestände waren zu Beginn des 20. Jahrhunderts ähnlich hoch wie heute, brachen aber in den 1930er Jahren infolge der Zwangskollektivierung der Nomaden zusammen. Sie erholten sich jedoch schnell und wuchsen in der Sowjetzeit stark an. Mit dem Zerfall der Sowjetunion brachen sie Anfang der 1990er Jahre zusammen, da staatliche Subventionen wegfielen und die Tiere in der ökonomischen Krise als Währung benutzt wurden. In den meisten Gebieten Kasachstans erholen sich die Viehbestände seit dem Jahr 2000 langsam. Die Beweidungsmuster waren zu Beginn des 20. Jahrhunderts noch von nomadischen Systemen geprägt, während zu Sowjetzeiten halbnomadische Ansätze vorherrschten. Seit Anfang der 1990er Jahre ist das Vieh nahezu ausschließlich um die Ortschaften konzentriert, da Mittel für Transport und Brunnenbau in der Steppe fehlen. Dies hat zu einer sehr ungleichmäßigen Beweidung der Steppe geführt.

Populationen wilder Huftiere wurden durch Überjagung früh dramatisch dezimiert, und die einzige Art, die in größerer Anzahl in der Steppenzone während des 20. Jahrhunderts überlebte, ist die Saiga-Antilope *Saiga tatarica*. Illegale Bejagung (zur Fleischgewinnung und zum Handel mit Hörnern, die als Aphrodisiakum in China stark nachgefragt werden) hat die Art an den Rand des Aussterbens gebracht: Ein Rückgang von über einer Million Tiere in den 1990er Jahren auf höchstens 30 000 im Jahre 2003 ist belegt.

Die Reaktionen von Steppenvögeln auf die beschriebenen tiefgreifenden Änderungen waren allgemein stark ausgeprägt. Im Rahmen einer großmaßstäbigen Modellierung von Vogeldichten entlang eines Landnutzungsgradienten in Zentralkasachstan (Kapitel 2) konnte ich zeigen, dass aufgegebene landwirtschaftliche Flächen und nicht oder schwach beweidete Steppen in naturnahem Zustand aktuell die größte Bedeutung für die meisten Steppenarten haben. Die schnelle Besiedlung und Bevorzugung aufgegebener Ackerflächen legt nahe, dass die Bestände vieler Steppenarten sich während der 1990er Jahre deutlich erholt haben, ganz im Gegensatz zur Situation in Mitteleuropa. Weitere Arten wie etwa die endemische Weißflügellerche *Melanocorypha leucoptera* oder der stark gefährdete Steppenkiebitz *Vanellus gregarius* scheinen stark von den Konzentrationseffekten in der Viehhaltung profitiert zu haben, die zu starkem Beweidungsdruck in kleinen Arealen geführt haben. Eine Analyse von Landnutzungsdaten der statistischen Ämter und quantitative Umfragen in landwirtschaftlichen Betrieben legen jedoch nahe, dass viele Arten aufgrund einer Umkehrung der beobachteten Landnutzungstrends in naher Zukunft wieder im Bestand abnehmen werden, vor allem infolge einer zunehmenden Reaktivierung brachliegender Flächen, einer bereits beobachtbaren Intensivierung in der Landwirtschaft, und einer fortschreitenden Rückkehr zu sowjetischen Beweidungssystemen.

Sich ändernde Beweidungsmuster, Abnahmen der Vieh- und wilden Huftierbestände, häufigere Steppenfeuer aufgrund stärkerer Biomasseakkumulation durch fehlende Beweidung und Nutzungsaufgabe führten zu starken Veränderungen der Steppenvegetation. Um zu verstehen, wie diese Prozesse Vogelgemeinschaften auf Mesoskalenebene beeinflussen, untersuchte ich die Einnischung von fünf Lerchenarten (der bei weitem dominierenden Steppenvogelgruppe) entlang zweier kontinuierlicher ökologischer Gradienten in der Steppe und Halbwüste Kasachstans (Kapitel 3): Beweidungsintensität und Zeit seit Nutzungsaufgabe von Weizenfeldern. Vegetationsstruktur und Pflanzenartenzusammensetzung variierten signifikant und nichtlinear entlang der Gradienten. Die untersuchten Lerchenarten reagierten ebenfalls nichtlinear auf Änderungen entlang der Gradienten und zeigten wenig Überlappung in ihren ökologischen Nischen: Mohrenlerche *Melanocorypha yeltoniensis*, Kalanderlerche *Melanocorypha calandra* und Feldlerche *Alauda arvensis* bevorzugten höhere und dichtere Vegetation, wie sie im Moment hauptsächlich auf aufgegebenen Äckern zu finden ist, während Weißflügellerche und Kurzzehenlerche *Calandrella brachydactyla* höhere Bestandsdichten in Gebieten mit einem höheren Anteil offenen Bodens und mehr Xerophyten erreichten. Die Lerchenbestände der Eurasischen Steppen und Halbwüsten haben generell wohl überwiegend von Nutzungsaufgabe und einer Abnahme der Beweidungsintensität profitiert. Die zu den Lerchen erhobenen Daten zeigen, dass Projektionen zukünftiger Bestandsänderungen (wie in Kapitel 2 vorgenommen) durch flexible Habitatmodellierungsansätze auf feineren Skalen deutlich verbessert werden können.

Noch weiter reichende Effekte von Landnutzungsänderungen ließen sich für den global als vom Aussterben bedroht eingestuften Steppenkiebitz nachweisen (Kapitel 4). Eine Konzentration von weidendem Vieh um die Siedlungen scheint in Kasachstan zu einer engen Bindung der Art an den Menschen (Synanthropie) geführt zu haben, die zur Sowjetzeit noch nicht beobachtet wurde. Auf Landschaftsebene waren Brutkolonien der Art stark an Siedlungen und Wasser gebunden, Habitatmodelle hatten eine hohe Vorhersagegüte und ließen nur 6.6 – 8.0 % des Untersuchungsgebietes als zur Brut geeignet erscheinen. Die hervorragende räumliche Übertragbarkeit der Modelle (getestet in einem Untersuchungsgebiet in Nordost-Kasachstan) deutet auf eine hohe Generalität der Ergebnisse für das gesamte Verbreitungsgebiet hin. Auf der Koloniеebene war die Antreffwahrscheinlichkeit eines Nests in den am stärksten beweideten Bereichen am höchsten, verbunden mit hohen Deckungsgraden von Viehdung und offenem Boden. Obwohl die menschliche Siedlungsdichte im Untersuchungsgebiet sehr niedrig ist, wurden die meisten Nester in Entfernungen von unter 2 km zum Siedlungsrand angelegt. Es konnte ein starker Zusammenhang zwischen der Beweidungsintensität und der Nestdichte der Steppenkiebitze nachgewiesen werden, und nur in Gebieten mit einer ausreichenden Mindestweidetierdichte wurden Brutkolonien gegründet. Diese Ergebnisse sind im Hinblick auf den starken Bestandrückgang der Art von hohem Wert und können für die Entwicklung von Habitatmanagementstrategien genutzt werden.

Eine ähnlich starke Bindung an weidendes Vieh ließ sich für die Schwarzflügel-Brachschwalbe *Glareola nordmanni* nachweisen, die im Laufe des 20. Jahrhunderts ebenfalls stark im Bestand zurückgegangen und daher auf der internationalen und europäischen Roten Liste zu finden ist. Die Gründe für diese Rückgänge liegen weitgehend im Dunkeln, da die Ökologie der Art bisher wenig untersucht war. Im Rahmen meiner Arbeit untersuchte ich Bruterfolg und Habitatwahl in zwei Untersuchungsgebieten in Kasachstan (Kapitel 5). Außerdem lege ich eine neue Schätzung des Weltbestandes vor, die unter Zuhilfenahme meiner eigenen Kartierungsdaten und russischsprachiger Literatur evaluiert wurde. Die Größe der Brutkolonien variierte von zweien bis 180 Paaren und war in Zentralkasachstan signifikant höher als in Nordostkasachstan. Die Antreffwahrscheinlichkeit war für Brutkolonien in der Nähe von menschlichen Siedlungen, bis 3 km von stehenden Gewässern und in Bereichen mit niedriger Vegetation am höchsten. Dies lässt auf eine Abhängigkeit von starker Beweidung und Wasser schließen. Der neu ermittelte Weltbestand von 76 000 – 95 000 Brutpaaren liegt deutlich höher als frühere Schätzungen und wurde von BirdLife International entsprechend korrigiert. Meine Ergebnisse lassen auf eine Bestandserholung der Art seit 1991 schließen, deren Gründe in einer Zunahme der Fläche aufgegebenen Ackerlandes und einer stärkeren Konzentration von Haustieren (die zu stärkerer Beweidung führt) liegen. Der Bestandrückgang zur Sowjetzeit wurde daher wahrscheinlich von einer gleichmäßigen Verteilung des Weideviehs über die Steppe ohne lokale Konzentrationseffekte und durch Habitatverluste durch Steppenumbruch verursacht.

Mit meiner Arbeit lege ich grundlegende Forschungsergebnisse zu Landnutzungswandel und Steppenvögel in Eurasien vor, die als Entscheidungshilfen in der Naturschutzplanung genutzt werden können. Konkrete Vorschläge umfassen die Einrichtung und Verbesserung von bestehenden Monitoringprogrammen, die Erarbeitung verbesserter Strategien zur Schutzgebietsauswahl und umfassende Lobbyarbeit auf politischer Ebene für nachhaltigere und naturnähere Landwirtschaft. Schlussendlich schlage ich Forschungsansätze vor, die die hier präsentierten Ergebnisse vertiefen und ergänzen könnten.

Краткое содержание

В данной диссертации я даю колличественную оценку изменениям в ведении сельского хозяйства, происшедшим на территории евразийских степей после распада Советского союза и оцениваю влияние этих изменений на сообщества и экологию птиц гнездящихся в степной зоне Казахстана.

В пределах евразийской степи основной отраслью сельского хозяйства является прежде всего зерновое хозяйство, с преобладанием посевов злаковых, и скотоводство. Уже рано началась распашка целины в Украине и европейской части России, где уже к концу 19-ого столетия почти не оста-

лось нетронутых участков степи. В Казахстане, значительные участки степи были рапаханы только в 50-е годы прошлого столетия, во время компании по ‘поднятию целины’. После распада Советского Союза, около половины сельхоз угодий степной зоны было заброшено во время приватизации государственной фермерской системы. Однако, экономический рост и рост цен на зерно, начиная с 2000 года, привели к широкомасштабному введению в севооборот залежных земель, одновременно с наблюдаемой в настоящие время интенсификацией и механизацией зернового хозяйства.

Численность скота была довольно высокой в начале 20-ого столетия, но резко сократилась в период коллестивизации в 1930 гг. Поголовье скота быстро восстановилось и сильно увеличилась в советские годы и снова сильно сократилось в период между 1993 и 1995 гг, так как государственные субсидии были приостановлены и домашние животные использовались в качестве наличных в годы экономического застоя. В большинстве регионов Казахстана, поголовье скота медленно, восстанавливается, но в некотрых регионах Казахстана и Южной России такого увеличения не наблюдается. В советский период характер выпаса изменился от кочевого к полу-кочевому, а после 1991 года скот концентрировался вокруг населенных пунктов, что привело к не сбалансированной нагрузке на степь.

Численность местных диких копытных резко сократилась под прессом охоты уже довольно давно и единственным видом, дожившим в значительном колличестве до 20-ого века была сайга *Saiga tatarica*. Однако в 1990-х годах процветала браконьерская охота на эту антелопу, вызванная огромным спросом на мясо и особенно рога (используемые в традиционной китайской медицине), что привело к 98 процентному сокращению численности к 2003 году, с одного более миллиона особей до лишь 30 тысячи особей. В целом, реакция популяций степных видов птиц на изменения в способах ведения земледения, вероятнее всего, была резко выраженной. В своей работе я смоделировал плотность населения птиц на большой территории типичного степного региона Центрального Казахстана, в пределах различных форм землепользования, от нетронутых степных участков, до посевов зерновых и участков с высокой пастбищной нагрузкой. Я показал, что старые залежи и нетронутая степь с отсутсвием выпаса были самыми важными местообитаниями для большинства видов птиц. Это дает основания предполагать, что благодаря прекращению посевного земледелия на больших территориях после 1991 го года, многие виды вошли в период значительного роста численности в 90-е годы и позже. Сконцентрированный выпас скота, приведший к образованию небольших участков с высокой пастбищной нагрузкой, также вероятно всего принес пользу ряду видов с высоким природоохранным приоритетом, таких как эндемичный белокрылый жаворонок *Melanocorypha leucoptera* или глобально угрожаемая кречетка *Vanellus gregarius.* Анализ статистики землепользования и целенаправленные социо-экономические исследования, проводимые среди земелепользователей, дают основания предполагать, что недавние и предсказываемые направления в сельском хозяйстве степной зоны, в частности возвращение в севооборот залежей зерновых и снижение патсбищной нагрузки, в близжайшем будущем могут вызвать сокращение численности большинства видов, включая ряд видов, ограниченных биомом. Я обсуждаю возможные решения, включая улучшение системы охраняемых территорий и возможность интенсивного земледелия только на части территории, оставляя остальные участки нетронутыми (‘land-sparing’).

Изменение системы выпаса, сокращение поголовья скота и диких копытных, учащение степных пожаров и отказ от земледелия на больших территориях – все это привело к радикальным изменениям растительности. Чтобы выяснить, как эти изменения повлияли на сообщества птиц, я провел оценку разделения по нишам видов жаворонков (Alaudidae), являющихся доминирующим семейством в пределах зоны евразийской степи (см. главу 3). Я изучил насколько распространение различных видов жаворонков в степной и полупустынной зонах Казахстана различается в отношении двух основных сельскохозяйственных факторов: интенсивность выпаса и возраст залежей злаковых. Структура растительности и ее состав значительно и не линейно отличались в зависимости от возраста залежей и различной плотности скота. Исследуемые виды жаворонков не линейно зависили от обоих факторов и показали высокую степень разделения по нишам. Как выяснилось, черный жаворонок *Melanocorypha yeltoniensis*, степной *Melanocorypha calandra* и полевой жаворонки предпочитают более густую и высокую растительность брошенных полей, в отличие от белокрылого и малого жаворонков *Calandrella brachydactyla*, которые были отмечены на участках с оголенной почвой и ксерофитной растительностью. В общем, появление залежных земель и снижение поголовья скота на огромных площадях степей и полупустынь стран бывшего Советского Союза, скорее всего, имело благоприятное влияние на численность жаворонков. Мои данные дают основания предполагать что анализ возможных изменений в степных сообществах птиц, основанных на прогнозах изменений основных типов местообитаний (как это было сделано в главе 2), может быть усовершенствован постредством лучшего понимания зависимости некоторых видов от более специфических факторов, относящихся к окружающей среде.

Путем моделирования связей местообитаний и распространения кречетки – глобально угрожаемого степного вида куликов в период гнездования (глава 4), я обнаружил еще более важные последствия изменений в землепользовании, которые в этом случае привели к высокой степени синантропности, вызванных измененениями в характере выпаса скота. На уровне ландшафта, гнездовые колонии кречекти значительно и положительно ассоциировались с наличием поселков и рек. Модели пригодности местообитания имели очень сильную прогнозирующую способность, предлагая лишь 6,6 – 8,0 % обследуемой территории площадью 30 000 кв км как потенциально подходящую для кречетки. Модели разработанные для описания распределения гнезд в одном регионе Казахстана, правильно предсказали распределение гнезд в другом регионе, что предполагает их хорошую преминимость к другим территориям. На уровне колонии, наиболее вероятное расположение гнезд обуславливается наличием участков с наиболее высокой пастбищной нагрузкой, наличием большого колличества навоза и участков с оголенной почвой. Несмотря на низкую плотность человеческих поселений на обследуемой территории, большинство гнезд кречетки располагались не далее 2 км от поселков. Проявлялась сильная зависимость между интенсивностью выпаса и плотностью гнезд кречетки, с явным пределом плотности выпаса, который нужно достигнуть, чтобы кречетка загнездилась. Эти выводы важны для разработки управленческих методов решения для улучшения природоохранного статуса этого угрожаемого степного кулика.

Как выяснилось, очень похожая сильная зависимость от домашнего скота характерна для степной тиркушки *Glareola nordmanni*, численность которой значительно сократилась в течении 20-го столетия, что привело к класификации этого вида как «близкий к угрожаемому» и «угрожаемый» в глобальной и европейской Красных книгах. Причины сокращения численность в большей степени не ясны, прежде всего из-за недостатка информации по гнездовой биологии данного вида. Я изучил успешность гнездования и использование местообитаний этого вида в двух регионах Казахстана и произвел новую оценку глобальной численности вида (глава 5). Размер колоний варьировал от двух до 180 пар и значительно отличался между исследуемыми участками. Так, например, средняя успешность гнездования в Централном Казахстане составила 1,30 ± 0,16 (среднее ± стандартная ошибка) летных птенцов на гнездовую пару; в Северо-Восточном Казахстане – 0,59 ± 0,13 летных птенцов на пару. Вероятность местонахождения гнездовых колоний была наибольшей поблизости от поселков, в пределах 3-х километров от открытой воды и на участках с короткой растительностью, что указывает на зависимость от выпаса и источников воды. Используя данные шести исследование со всего гнездового ареала, я рассчитал новую мировую оценку численности, составившую 76 000 – 95 000 гнездовых пар, что значительно выше чем предыдущие оценки, принятые BirdLife International. Я предполагаю что площадь пригодных местообитаний для тиркушки существенно увеличилась за счет увеличения площадей залежных земель и изменения характера выпаса в годы после распада Советского Союза в 1991 году.

В своей диссертации я представляю исходные данные для направления решений в области охраны птиц, предоставляя возможность для разработки природоохранных стратегий, имеющих максимальную выгоду для биоразнообразия, без негативного влияния на жизненные стандарты местного населения. Я предлагаю усовершенствование мониторинга биоразнообразия и изменений в землепользовании, а также схемы выбора территорий для заповедников и делаю вывод, что уже сейчас необходимо лоббирование в государственных органах Казахстана в пользу более ‘зеленого‘ фермерства. В заключение, я предлагаю возможности дальнейших исследований и определяю существующие пробелы в знаниях.

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