Conserving a moving target: planning protection for a migratory species as its distribution changes

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Running title: Landscape-scale planning for a migratory species

Word count: 7793 words (Summary to References inclusive)
Summary

1. Conservation of declining migratory species is a challenging task, as the factors that may have determined their past distribution may not determine their current and future distribution. Saiga antelope populations have massively declined due to poaching. The species is now beginning to recover in Kazakhstan and protected areas (PAs) are being implemented. Using 25 years of aerial monitoring data, we identified changes in the spring distribution and predicted densities of saiga to prioritize areas for protection under scenarios of climate change together with changes in disturbance and population size. Conserving the spring distribution is critical as spring calving aggregations are of particular importance to population viability.

2. The current distribution is strongly influenced by disturbance, whereas climate had a stronger influence in the past. The area of highly suitable habitat has halved and become fragmented in the last decade. The existing and proposed PAs are relatively complementary and perform well under most scenarios of future change. However there is a need to widen the geographical scope of PA planning if potential future high suitability areas are to be effectively protected.

3. Climate change interacts with other factors to determine the distribution of suitable habitat within and outside PAs. Scenarios in which conservation has increased saiga population size and density tend to show limited impacts of climate change, while scenarios in which the saiga population fails to recover and disturbance continues show worsening patchiness and reduced suitable habitat.

4. Synthesis and applications: We provide evidence for changing distribution and density of a migratory species over a large spatio-temporal scale, and suggest that future distribution may be more constrained and spatially heterogeneous. These results have important implications for designing future conservation measures for migratory species, such that areas...
that robustly show high suitability under a range of potential scenarios of change can be
included in PA expansion plans. PA placement based only on current, rather than projected
distribution risks wasting opportunities for proactive conservation, particularly for a highly
disturbed, recovering species likely to be affected by climate change.

Key words – conservation planning, climate change, GAMM, HSM, long distance migration,
NDVI, poaching, protected areas, Saiga tatarica tatarica, ungulates.
Introduction

Many ungulate migrations worldwide have been disrupted in the last two centuries due to human impacts (Bolger et al. 2008; Harris et al. 2009). Several studies have raised concern over the plight of migratory species and urged the need for proper monitoring and establishment of protected areas (Bolger et al. 2008; Harris et al. 2009). However, protection of such species is challenging because the animals occur in large numbers, are frequently on the move and are distributed over vast areas (Mueller et al. 2008). Often, migratory routes vary by season and year, which makes establishment of static protected areas (PAs) challenging. Many migratory ungulates are also subjected to poaching and habitat modification, which cause changes in habitat use (Shuter et al. in press). The prioritization of survey areas and protected area planning can become difficult in such situations, especially for species whose populations have declined substantially and so are potentially not currently occupying typical habitat.

The issue of climate change has received significant attention recently, as it is expected to induce major changes in migratory systems and hence raise further challenges to the management of migratory species (Lundberg & Moberg 2003; Hodgson et al. 2009). Especially in the case of migratory ungulates for which the timing of spring green up is tightly coupled with the onset of the spring migration and dense calving aggregations, climatic changes in temperature and productivity are likely to induce major range shifts during spring (Lundberg & Moberg 2003; Singh et al. 2010a & b; Wilcove & Wikelski 2008). This implies that an understanding of the drivers of the spring distribution of these species is particularly important for conservation planning. Pressey et al. (2007) suggest that effective conservation planning must recognise both the inherent dynamism of ecological processes and the effects of anthropogenic alterations on habitat use and availability.
Following on from this, there is a need to integrate uncertainty into spatial predictions of species presence and to make precautionary decisions that avoid underestimating threats. Decisions also need to be regularly revisited in the light of novel and potential threats (Wilson et al. 2007). It is also important to evaluate the effects of conservation on future species distributions, in the light of ongoing environmental change. When planning responses to climate change scenarios, Wiens & Bachelet (2010) urge conservationists to align the scale of conservation action to the scales of climate change projections.

An additional challenge is the uncertainty in identification of important habitats for threatened or declining species. Freckleton et al. (2006) explored the likely relationship between population density and occupancy and found that a generally positive relationship, but that departures from this relationship were potentially informative as to population status. Especially for endangered or declining species, there may not always be a linear relationship between occurrence and abundance. Predicting the spatial relationship between density and occupancy is hence potentially important in evaluating the proportion of the population likely to benefit from particular PAs. Effective stratification of population monitoring also depends upon an understanding of the relationship between the density and distribution of a population.

An excellent example of a species facing these issues is the migratory saiga antelope (Saiga tatarica) of Central Asia, which has experienced a 95% reduction in population size over the last two decades (Milner-Gulland et al. 2001; 2003). Simultaneously, group sizes have decreased (McConville et al. 2009), density has decreased and sex ratio and conception rates (Milner-Gulland et al. 2003) and the location and density of calving aggregations have both been affected by human disturbance (Fry 2004; Singh et al. 2010a). For the last four decades, annual aerial surveys have been conducted over the spring range of saiga in Kazakhstan to estimate population size, density and identify aggregations. Considerable
conservation efforts are now being undertaken for saiga on a landscape scale, mostly within
the spring range. For example the Altyn Dala Conservation Initiative (ADCI) is working in
Central Kazakhstan, carrying out activities such as research, community engagement, anti-
poaching patrols, improvement of monitoring and the designation of new PAs (Klebelsberg
2008). As a result of investment in initiatives such as these by the Government of Kazakhstan
and international NGOs, saigas are currently recovering rapidly in this region, and new PAs
are being planned and implemented (CMS 2010). Under these circumstances, it is essential
that the designation of PAs, which consumes substantial time, resources, and legislative
activity, is based on best estimates of the future needs of the species. The regional predictions
for Kazakhstan from global climate change models predict precipitation changes and an
increase in spring temperature in the region (IPCC 2007). Recent studies based on analysis of
time series satellite data also predict a decline in productivity across the saiga range (de Beurs
et al. 2009, Zhao & Running 2010). Kazakhstan is currently undergoing rapid development,
including new infrastructure, urban growth and human population increases, which are likely
to change patterns of human disturbance, and together with increasing wealth, may affect
poaching pressure (Kühl et al. 2009). These changes will combine to affect saiga densities
and distribution in future, which may render PAs based upon current saiga presence less well
targeted than they could be.

Long term aerial survey data provide a unique opportunity to identify changes in
spring saiga distribution patterns and to assess the adequacy of different protected area plans
(Singh et. al. 2010a & b). We used the last 25 years of aerial survey data to identify the
changing drivers of saiga distribution in Central Kazakhstan. We analyzed trends in
distribution patterns, explored factors affecting the spring distribution, and then identified
areas of high potential saiga density, where monitoring and protection could be focused. We
compared density and occupancy predictions to identify areas of mismatch between the two.
Since future changes in climate and human activities may cause changes in saiga distribution, we projected the current distribution under a range of scenarios, based on IPCC projections of spring temperature rise and vegetation productivity changes in the region (IPCC 2007), in combination with assumptions about the success or failure of current conservation interventions in reducing human disturbance. We then evaluated the location of current and planned PAs with respect to potential future spring saiga distributions. This approach provides a robust basis for the continuing conservation planning process in Central Kazakhstan, as well as providing guidance for similar studies on other migratory species. It fills an important gap in the existing literature on modelling the effects of climate and anthropogenic factors to understand their synergistic impact on species density and distribution.

### Study area and methods

#### Study area

We consider the Betpak Dala saiga population, located in central Kazakhstan. This was historically both the largest and the widest ranging of the four populations of sub-species *S.t. tatarica*, covering an estimated area of about 1.08 million km². The area is generally flat, covered by treeless steppe, semi-desert and desert vegetation. Vegetation zones occur in a latitudinal gradient. The northernmost steppe zone is followed by semi desert and desert zones with annual precipitation of around 300 mm, 200–250 mm and <200 mm, respectively. Saigas inhabit all three zones on a seasonal basis (Fadeev & Sludskiy 1982; Bekenov *et al.* 1998). Their annual migrations, 600-1200 km in length, are driven by the need for new green pastures in the spring (March-May) and by the presence of deep snow in the steppe zone starting in autumn (September–October). The area in which spring calving was historically observed in this population is 400 km in length north-south and 700 km east-west (Bekenov
et al. 1998). The period, route, distance and speed of migration differ from year to year depending on climatic conditions, the condition of pastures, the number of watering places and the degree of disturbance experienced by the animals (Bekenov et al. 1998; Singh et al. 2010a).

This population was severely and rapidly affected by poaching due to its relative accessibility from the capital Almaty and from the main saiga horn markets in China. The population declined from an estimated 375,000 animals in the 1980s to an estimated 1,800 at its nadir in 2003 (although this is likely to be a substantial underestimate; McConville et al. 2009). The 2010 population estimate is 53,400, around 14% of the 1980s size, but substantially larger than only a few years previously (CMS 2010; Figure S1). This population has been the recipient of significant conservation action, which is likely to be one reason for its rapid recovery.

Aerial survey data

We acquired aerial survey reports from the Institute of Zoology of Kazakhstan for the period 1983-2008, with some years missing (1984, 1990, 1998 and 2000). These reports contain information on the dates and timing of aerial surveys, the areas surveyed, locations of the groups with ~500m resolution, group sizes observed and the population estimates made (see Figure S2 for an example of the maps generated). These observations were transferred into a Geographic Information System. The survey technique was developed during Soviet times and remained unchanged throughout the study period. The aerial survey team flew transects over the areas of highest saiga density, determined through local and expert knowledge. Transects were, where possible, 10 km apart and the assumed strip width was 1 km each side of the aircraft, such that 20% of the area was covered. The estimated size and approximate location of each group seen and were marked on a topographic map of scale 1:1,000,000. The
team then extrapolated the population estimate by dividing the number of saiga seen by the coverage (usually 0.2) and multiplying by the size of the area of saiga concentration, calculated by drawing a line around the observations and counting grid squares within that line. There was no measure of error.

The population crash towards the end of the 1990s led to a change in the group size distribution, which affected the population estimates. Formerly, saiga aggregated in large numbers during the spring migration, with approximately 40% of the groups containing over 500 individuals (Fadeev & Sludskii 1982). This changed considerably in recent years, with maximum herd sizes in the low hundreds, and the majority of herds numbering less than 50 (Institute of Zoology, unpublished data). The extent to which these changes have affected the bias in the population estimates is unclear but potentially significant (McConville et al. 2009). Significant issues with the sampling procedures have also recently been identified (Norton-Griffiths & McConville 2007), which are now being addressed (Zuther 2009).

**Variables**

The spring distribution of saiga is determined by temperature, availability of water and green forage (Bekenov et al. 1998; Singh et al. 2010b). We selected mean diurnal range of temperature during the survey period (March-May), vegetation productivity and distance to water and settlements as predictor variables. Singh et al. (2010b) showed for the whole of Kazakhstan that all these variables were important determinants of saiga presence/absence in spring. We used temperature range as it made sense biologically and was a better fit to the data than other temperature metrics. In early spring the maximum temperature may be influential in the onset of spring migration as a result of snow melt, but later in the period, during calving, survival of new born saiga calves is limited by minimum temperature (Milner-Gulland 1994; Bekenov et al. 1998). Mean diurnal range of temperature, henceforth
“temperature” was estimated from monthly maximum and minimum temperature data for the survey period, obtained from the National Climate Data Center (ftp://ftp.ncdc.noaa.gov/pub/data/ghcn/v2). These data were obtained from various ground stations and were gridded to be used as raster layers with 1km² resolution (http://www.esrl.noaa.gov/psd/data/gridded/). We rescaled all the variables to a pixel size of 25 km², since the scale of the aerial survey is large and groups are spread over vast areas.

We used vegetation productivity instead of precipitation as these two variables are confounded (Singh et al. 2010a). We used the Integrated Normalized Difference Vegetation Index (INDVI) as an index of vegetation productivity (Pettorelli et al. 2006). We acquired NDVI data from 15-day GIMMS (Global Inventory Modelling and Mapping Studies) dataset (8 km² spatial resolution - ftp://ftp.glef.umiacs.umd.edu/glef/GIMMS/Geographic/; Tucker et al. 2005) and from the bimonthly MODIS dataset (for years 2007-08, 1 km resolution; Global Land Cover Facility, https://wist.echo.nasa.gov/wist-bin/api/ims.cgi?mode=MAINSRCH&JS=1) resampled to the scale of GIMMS data as GIMMS was only available up to 2006. We estimated INDVI as the sum of NDVI from March to mid May, because the aerial surveys were conducted towards the end of April and first half of May. The straight line distance to the nearest natural water and settlements were estimated for each calving location based on maps acquired from ‘Biogeomancer project’ (http://www.biogeomancer.org/) for water and ‘Global database on Administrative areas’ (http://biogeo.berkeley.edu/gadm/) for settlements. Both temporary and permanent water sources were included, because temporary water sources are full in spring. The straight-line distance to the nearest settlement in the database was regarded as an indicator of the level of disturbance due to poaching pressure. Settlement location has remained consistent in the region over the period, despite changes in settlement size, and poaching pressure is not likely
to be straightforwardly frequency dependent (Kühl et al. 2009), hence the size of the settlement was not included.

**Saiga distribution modelling**

Habitat suitability models (HSMs) apply ecological niche principles, using environmental variables to predict the presence/absence or abundance of a species throughout a study area, with the primary aim of identifying key variables that determine the niche (Hirzel & LeLay 2008). However, the strength of the distribution-niche linkage depends on the ecology of the species, local constraints and historical events (Hirzel & Le Lay 2008). We hence tested five different modelling approaches, consisting of both presence-pseudo absence and presence only methods, to select the best approach for modelling annual saiga distributions based on climatic and anthropogenic variables (Table S1; Thuiller et al. 2009). A presence-pseudo-absence approach using logistic Generalized Additive Models (GAM) with a binary response variable and continuous explanatory variables consistently performed better than other methods based on AUC values (Hastie & Tibshirani 1990, Table S1). We therefore used this approach instead of a presence-only approach such as Ecological Niche Factor Analysis (ENFA) or Maxent as they over-predicted suitable habitat, as has been observed in other studies (Chefaoui & Lobo 2007; Matthiopoulos & Aarts 2010). We generated 2000 pseudo-absences randomly within the annual range area of the Betpak Dala population, of which 1890 were left after removing the points from water bodies.

After estimating the yearly models, we tested whether pooling the data into three periods would be more representative of the changes over the study period. This was done to overcome the high yearly variability in saiga locations, probably a result of the confounded effects of weather and observer bias. The yearly observations were pooled into 3 periods- Period I: 1986 to 1996, II: 1997 to 2002 and III: 2003-2008, representing three different saiga
population states; I - high and relatively stable, II- declining and III - low/recovering (Figure S1). We ran these models using generalized additive mixed models with a cubic spline smoother value of 3 (GAMMS; Wood 2004), year as the random effect and other explanatory variables as fixed effects (Table S2). We accounted for spatial autocorrelation by incorporating ‘X’ and ‘Y’ coordinates of the centroids of the saiga group locations as fixed effects. Spatial predictions were made for all three periods and models were validated using k-folds cross validation (Boyce et al. 2002). We used <0.2, 0.2-0.5 and >0.5 suitability thresholds to classify the predictions into low, medium and high suitability areas. To estimate variable contributions we first estimated the correlation score between the standard predictions versus the predictions of the model from a randomly permutated variable (Thuiller et al. 2009). We then estimated 1 minus the mean correlation for each variable where a high score meant a high importance. The results were then converted to give a relative importance (summing to one; Thuiller et al. 2009).

Change scenarios

The best model for period III as the current baseline was used to test the effects of potential future changes on saiga distribution. Two dimensions of change were explored; climate change leading to a rise in spring temperature and/or reduced vegetation productivity, and anthropogenic change leading to increased or reduced disturbance and/or increases in population and group size. We manipulated the dataset and environmental variables keeping the model structure constant, to get a general idea of the consequent distributional changes. The main scenarios tested were (Table 1): T+: Temperature + 2.5°C, modelled by creating a future temperature layer using the predicted rise in maximum spring temperature from the 2007 IPCC report. N-: NDVI -13.5% due to increased droughts, based on predictions for the area in de Beurs et al. (2009) and Zhao & Running (2010), modelled similarly to the T+
scenario. D+: Increased disturbance; in this scenario saigas may move further away from towns, hence each saiga observation was moved 4 km further away from the nearest town than its observed location. The value of 4 km was chosen based on the observed shift of saiga groups away from settlements between periods I and III (Table S2). D-: Disturbance decreases; we decreased the distance of observations from the nearest settlement to Period I levels (i.e. by 4 km). P+: Population recovers to 150,000 (based upon the Government of Kazakhstan’s goal to increase saiga numbers in Kazakhstan to 200,000 in the next 10 years, and because the Betpak Dala population is the only one that is currently increasing rapidly). We increased the frequency of all group sizes in the database equivalently, to mimic an increased population size but the same group size distribution as currently. G+: Population recovers and also becomes less fragmented (based upon the fact that group sizes were very much larger in previous periods than in period III): We increased the population size to 150,000 by increasing the number of saigas in the top 10% of group sizes. Finally, we combined some of the scenarios to give composite scenarios that included the most likely potential combinations of effects. These composites included one that mimicked conservation success, in which disturbance was reduced and the population increased, with a concomitant increase in mean group size, but in the context of climate change (T+P-D-G+), and one mimicking conservation failure, in which disturbance increased and the population stayed at the current level (T+P-D+; Table 1).

Future protected area (PA) evaluation

To assess the relevance of existing and proposed PAs to potential future distributions, we mapped the two existing and three proposed PAs in the Betpak Dala population’s spring range, based on information from the Association for the Conservation of Biodiversity in Kazakhstan (ACBK; www.acbk.kz; Figure S3) and the United Nations Development
Programme’s Steppe Conservation Project (www.undp.kz). We overlaid this map over our model predictions for period I (representing healthy saiga populations in the past), period III (representing the current situation) and for the future change scenarios, then identified the suitable habitat falling under each PA type. We considered five PAs of which two already exist, and three are proposed (Figure S3). The total area covered by these PAs is 20,250 km², made up of 14,681 km² of existing PAs and 5,568 km² of proposed PAs, compared to the identified current spring saiga range of about 650,000 km². We then estimated the proportion of the PA area with high (>0.5), medium (0.2-0.5) and low (<0.2) habitat suitability. We also estimated the proportion of each of these suitability types within the PAs versus in the entire spring range.

**Predicting future density**

We predicted the spatial distribution of saiga density, to compare the distribution of density and occupancy, understand model limitations and identify which model is a better metric for future scenarios. Predicted relationships for period III and the future scenarios could also be used to guide the allocation of monitoring and protection efforts to areas of high saiga density. The aerial survey data included information about group size and extent from which density could be inferred. However, observed group size distribution from Kazakhstan’s aerial surveys are likely to be severely biased by observation error, artificially reducing the number of small groups in the dataset (McConville et al. 2009). Hence we reconstructed putative original group size distributions using the bias correction algorithm developed by McConville et al. (2009), obtaining an estimate and range of corrected group sizes for each year. We assumed the total population size and then back-calculated the actual group size distribution using log-normal curves. This distribution was then corrected using the
detectibility function used by McConville et al. (2009) and was simulated 100 times for each year to be used in the models of density distribution.

Once the bias-corrected group size distribution had been obtained from the original survey data, we fitted a kernel density estimator to our observed point pattern with a smoothing parameter estimated using cross validation (Baddeley 2008; Hengl et al. 2009). We fitted the relative density as a ratio between the local density and maximum density from all locations (Hengl et al. 2009; Hengl 2009). The advantage of using the relative density is that the values are in the range [0, 1], regardless of the bandwidth and sample size. We then used the logistic regression kriging technique from Hengl et al. (2009) to predict saiga group density by: (1) converting the group sizes to logits (if the input values are equal to 0 or 1, replacing them with the second smallest/highest value); (2) fitting a regression model (GAMM in our case) with temperature, NDVI, distance to towns and water as explanatory variables, based on the variables found important in previous modelling exercises (Singh et al. 2010a & b and the distribution model in this paper); (3) fitting a variogram for the residuals (logits); (4) producing predictions by first predicting the regression model part, then interpolating the residuals using ordinary kriging, and finally adding the predicted trend and residuals together; (5) back-transforming the interpolated logits to the original (0, 1) scale. We performed these analyses for period III. The density predictions were then stratified into three strata based on the predicted density of the groups (<0.02, 0.02-0.05, >0.05 animals / km²).

To identify the relationship between predicted density and occupancy of saiga, we used mean density and mean habitat suitability for each pixel and estimated the product-moment correlations (Freckleton et al. 2006).
Results

Saiga distribution modelling

The spring saiga distribution was determined by an intermediate range of temperature, intermediate productivity, areas at intermediate distance from water and away from settlements. The yearly models demonstrate a high variability in the percentage contribution of these variables, with temperature consistently explaining most of the variability, while other variables varied in time (Figure S4). The periodic models captured the same consistency (Table S2), but were more robust to interannual variation, and so were used for the scenario analyses in preference to the yearly models. In period I, temperature explained most variation in group location (52.8%) followed by NDVI (15.8%; Figure 1, Table S2). For period II, the trends were similar, with temperature and NDVI still explaining most of the variability (Temperature- 51.3% NDVI- 11.0%), but the contribution of distance to settlements slightly increased (from 2.35 to 6.7%). However during period III, the contribution of temperature and NDVI declined (29.5 and 13.9% respectively) while distance to settlements increased substantially (22.6%, Figure 1). Percentage variation explained by spatial autocorrelation of groups was 9.9% and by year, about 15.1%. There was no significant spatial autocorrelation observed in spatial variograms of the residuals. The high Spearman rank correlation coefficients from cross validations for each model showed that the models had good predictive ability (Table S3).

There was a 50% decline in the amount of high suitability area in period III compared to period I and a slight decline compared to period II. The extent of medium suitability areas increased by about 25% in period III compared to period I (Figure 2).
Change scenarios

The predictions from the different scenarios were highly variable both in terms of the quantity and spatial distribution of suitable habitat. A 60% loss in high and 80% loss in medium suitability areas was predicted with rising temperatures, with patchier spatial occurrence of high suitability areas (Table 1, Figure S5). A decline in productivity had less effect on the total amount of each habitat type, but increased the patchiness of the distribution (Table 1, Figure S5). Increasing disturbance had a particularly strong effect in the northwest, whereas decreased disturbance lead to consolidation of the distribution, with both high and low probability habitat gaining at the expense of the medium probability habitat. Similar, and more extreme, consolidation within high probability areas was seen in the population increase scenarios, with a reduction in group fragmentation in particular leading to more than half of the occupied saiga range having a high suitability. The climate-only combined scenario, T+N- led to a shift in the distribution to the south and east, with large areas of the northern part of the spring range becoming low probability. Including the anthropogenic factors into either a “best” or “worst” conservation scenario illustrated that population fragmentation and the location of the areas of high probability of presence were strongly dependent on the outcome of conservation, although this effect was modulated by the predicted changes in climate. “Conservation success” lead to a homogenous distribution similar to period I, whereas “conservation failure” lead to a widely distributed, patchy population. In all three combined scenarios, there was more high probability habitat in the southeast part of the range than currently, and less in the north-west.

Future protected area (PA) evaluation

The current PA system was more effective at protecting current, rather than past, high suitability areas, with the proportion of current high suitability habitat within the PA system
being 23%, compared to 8% under the period I saiga distribution (Table 2, Figure 3a & b). However it was not substantially better than random placement within the spring range, as 17% of the current spring range was rated as high suitability (Table 2). If the proposed PAs were added, the proportion of current high suitability habitat in PAs would be much improved, to 43%. The current PA system performed much better than random under increased disturbance (62% high suitability habitat), whereas the proposed PAs performed best under reduced disturbance and increased population size. The proposed PAs performed very differently to the existing PAs in some scenarios, which suggested a degree of complementarity which may enhance robustness to uncertainty. For example under reduced productivity, the proposed PAs performed very badly (11%) and existing PAs improved their performance (to 27%), while if the population became larger and less fragmented, proposed PAs remained effective (75%) while existing ones performed very badly (8%). This was due to changing distributions under these different scenarios (Figures 3c, 3d & S5). The PA system performed relatively poorly under all three of the combined scenarios; in all cases the combined performance dropped below current levels, substantially so in the case of conservation failure (43% high probability habitat currently, 24% projected). The actual coverage of the existing and proposed PA system was low, which was expected given the very large areas involved; the percentage of the total high quality habitat currently covered by the existing PAs was only 1%, with an additional 2% in the proposed PAs (Table S4).

**Predicting future density**

The density models from periods I and III produced similar results to the occupancy models, where distance to towns explained most of the variation in the model in Period III. The regression-kriging model explained 91% of the original variation and predicted densities well (Table S5). The maximum observed densities were 0.08 animals/km² for Period I, with the
groups spread in a relatively homogeneous line at a constant latitude (Figure 4a). The stratified map of current (period III) predicted highest density showed at least three major areas of high density for saiga in the spring range, near the towns of Turgay, Irgiz and Zhezkazgan (Figure 4b). The high density areas were shifted north and west compared to Period I. For the conservation failure scenario (T+N-D+; Figure 4c), the predicted density was much lower on average, at 0.02 animals/km² and the high density areas were more centrally located. In the conservation success scenario (T+N-D-G+; Figure 4d), with a density of 0.09 animals/km², the population was similar in distribution to Period III, but with high density areas reappearing in the east. However the results for the conservation success scenario suffer from a degree of circularity, given the assumption of population increase being concentrated in the largest herd sizes.

Density-distribution relationships

The distribution of habitat suitability was bimodal for period I, whereas for period III and the two conservation scenarios it was left skewed (Figure S7). There was a significant positive relationship between mean density and occupancy for all the models (Period I - $r_s = 0.458$, n=1998, $p < 0.001$; Period III- $r_s = 0.876$, n=1998, $p<0.001$; Conservation success- $r_s = 0.785$, n=1998, $p < 0.001$; Conservation failure - $r_s = 0.434$, n=1998, $p<0.001$). In period III and under the conservation success scenario, the strong correlations were matched by a strong spatial overlap between high density areas and areas with a high probability of occupancy (Figure. S8). However in period I, when the population was large and healthy, there was a substantial swathe of the south of the range which was highly likely to be occupied, but where density was not predicted to be high. In the conservation failure scenario, with more disturbed and fragmented populations, areas of predicted high occupancy were also spatially
Discussion

Saigas show a similar pattern to other long distance migratory ungulates, where the spring migration is driven by a rise in temperatures and an increase in productivity (Bolger et al. 2008; Singh et al. 2010a). Suitable habitat in the spring range is characterized by intermediate temperatures and productivity, is an intermediate distance from water and away from settlements. Temperature is a limiting factor for the survival of new born calves in spring, which may drive the role of temperature in defining suitable habitat (Bekenov et al. 1998). With suitable habitat characterized by intermediate productivity, saiga may trade off forage quantity for quality, as observed in several other migratory ungulates (Mueller et al. 2008; Hebblewhite et al. 2008; Holdo et al. 2009). Sites at an intermediate distance from water may indicate avoidance of disturbance from other animals, predators and humans, which also use water bodies. Moreover, availability of water may not be limiting in spring, when precipitation is relatively high. Finally, sites away from settlements and an increase in the role of this variable with time clearly indicates avoidance of areas with high disturbance (Singh et al. 2010b), although it is not possible to determine whether this is because at low population sizes there is no need to approach settlements in order to access high quality habitat, or whether increased disturbance in recent years has driven saigas away from otherwise high quality areas.

As expected, the scenarios of future change lead to significant predicted changes in saiga spring distribution. Climate change was predicted to reduce the extent of highly suitable habitat, and produce a more heterogeneous pattern of habitat. It was also predicted to lead to
shifts in highly suitable habitat with increases in some areas (especially the south east) and
decreases in others (the northwest). This may have implications for migratory routes,
foraging behaviour and selection of favourable areas for calving. An indirect effect on
population productivity might be expected. These likely effects of climate change are similar
to those predicted for other migratory species (Lundberg & Moberg 2003; Shuter et al. in
press), but in our study we have been able to characterise potential changes spatially and in
more detail than is commonly possible. It has also been instructive to consider how
conservation outcomes may interact with climate change; successful conservation tends to
mitigate the effects of climate change, while conservation failure exacerbates the patchiness
and loss of suitable habitat. For the saiga, as is likely for many similar species (Harris et al.
2009), disturbance currently overrides the contribution of other variables. This suggests that a
conservation priority should be to reduce the effects of human disturbance in otherwise
highly suitable areas, for example by reducing poaching levels, limiting human use of natural
watering places or restricting entry to areas of high saiga density such as calving
aggregations.

Currently, only a few PAs exist in the vast spring range of the Betpak Dala saiga population,
covering only 1.05% of the current high suitability areas (Figure S3). This is a typical picture
for migratory species which cover large areas during their long-range movements (Harris et
al. 2009). A particular concern for saigas is that the current and planned PAs are concentrated
in the north-west of the spring range, where saiga are currently at high density. However, the
eastern parts of the range were important in the 1980s and could be again, as populations
increase. The eastern areas were particularly prominent in our more realistic combined
scenarios. It is important to aim for geographic representativeness when planning PAs
(Hodgson et al. 2009), and our analyses demonstrate that if making PAs robust to plausible
future scenarios is also an aim (Pressey *et al.* 2007; Hannah 2008), a priority should be to improve PA coverage in areas of past and predicted high density in the east.

Our study only considers the spring range, prior to calving, because this is when the available data were collected. The winter range of the saiga is under-represented in the PA system at present with only one protected area, and no new PAs are proposed for this area. However, the winter period is also critical for the saiga, as the winter range is more limited in extent than the other seasonal ranges and is shared with livestock, with the potential for food limitation as well as direct mortality from harsh weather (Sludsky 1963; Bekenov *et al.* 1998; Coulson *et al.* 2001). There is an urgent need for similar analyses to be conducted within the winter range, but this requires data on saiga distribution at this time of year, which are currently lacking. GPS collars could provide an effective way to gather this data, given the difficulties of aerial and ground surveys in the winter months.

The recent and potential increases in patchiness of saiga distributions have important implications for monitoring, since surveying patchy distributions entails increased cost and lower reliability. In such a situation, our predicted density maps may be useful in guiding monitoring efforts towards high density areas. Our results showed a significantly positive relationship between predicted density and occupancy for a migratory species in a variety of circumstances ranging from a healthy and abundant population phase to a critically endangered low density phase. However, the spatial mismatches observed in the healthy population phase and conservation failure scenario showed that such relationships may not follow a consistent pattern at large spatial and temporal scales and as population status changes. Freckleton *et al.* (2006) showed that when habitat suitability was left-skewed, density–occupancy relationships were positive and linear, whereas for bimodal distributions, the relationships were weak; this finding was echoed in our study. Models of habitat
suitability based on data collected from disturbed populations may be misleading if density and occupancy are assumed to be proxies for each other. Overall, however, the positive relationships between density and occupancy which we found suggested that either may be useful when designing protected areas or monitoring strategies.

**Management implications**

Work of the type presented here is crucial in providing baselines for landscape-scale conservation initiatives. An approach such as ours may ensure that monitoring remains cost effective and that PA networks are robust to future changes in distribution and densities of key target species. Here we have used the available data to model the likelihood of saiga presence and density in a particular season in a spatially explicit manner. This is a fundamental requirement for embarking on a systematic conservation planning process. We have also made some extrapolations to the future, based upon realistic scenarios. These are crude, and assume that the structure of the models governing current distribution remains the same as conditions change and as we extrapolate away from the data. However they are the best we have currently available and can give general indications of the effectiveness of current and proposed PAs for saiga conservation at the landscape and decadal scales.

This approach also has broad resonance for the conservation of similar long distance migratory species. A dynamic predictive approach that both assesses past and current drivers of distribution and predicts future distribution under plausible scenarios is more robust than relying on current status. It can provide insights into the contrasting drivers of current, potentially highly disrupted and fragmented distributions, and of healthier populations in the past. One potential application of the scenario-based approach is evaluation of conservation interventions against a spatially explicit set of objectives. For example, a PA network might
be planned to ensure that it contains more than a threshold level of predicted high quality habitat under a range of likely scenarios of environmental and anthropogenic change.

Acknowledgements

We would like to thank the Institute of Zoology, Almaty, Kazakhstan for providing access to their long term datasets and especially Dr. Iu. A. Grachev and Dr. A.B. Bekenov for hosting NJS in Almaty. This work was supported by the Leverhulme Trust and by a Royal Society Wolfson Research Merit Award to EJMG. Thanks to Joaquin Hortal, Miguel Á Olalla-Tárraga, Steffen Zuther and Nils Bunnefeld for helpful comments. Mark Hebblewhite, Julia Jones and one anonymous reviewer also provided valuable comments that greatly improved the manuscript.

References


Table 1. Percent area under three habitat suitability categories of predicted saiga presence for 9 different change scenarios. Period III is the current situation. **T+**: Temperature increases by 2.5°C; **N-**: NDVI decreases by 13.5%; **D+**: Disturbance increases by 4 km (i.e. more people or more hunting); **D-**: Disturbance – to 1980s levels (conservation programmes succeed); **P+**: Population increases to 150,000; **G+**: Population increases and groups become less fragmented. Combined scenarios include climate change only (T+N-), climate change with increased disturbance (“conservation failure”; T+N-D+), and climate change with decreased disturbance and a larger, less fragmented population (“conservation success”, T+N-D-G+).

<table>
<thead>
<tr>
<th></th>
<th>Period III</th>
<th>T+</th>
<th>N-</th>
<th>D+</th>
<th>D-</th>
<th>P+</th>
<th>G+</th>
<th>T+ N-</th>
<th>T+N- D+</th>
<th>T+N-D-G+</th>
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<tr>
<td></td>
<td></td>
<td>16.84</td>
<td>6.96</td>
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<td>13.50</td>
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<td>6.73</td>
<td>56.28</td>
<td>39.26</td>
<td>20.14</td>
<td>40.67</td>
<td>33.27</td>
<td>21.60</td>
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<tr>
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<td>86.31</td>
<td>30.58</td>
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<td>16.90</td>
<td>15.61</td>
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Table 2. Percentage of High, Medium and Low probability habitat occurring within current PAs, proposed PAs, and current and proposed PAs combined (‘Total’), compared to the Predicted Total Area of each habitat type in the saiga spring range for Periods I and III and 9 future scenarios (see Table 1 for scenario explanations). The values are rounded to the nearest whole number.

<table>
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<th>Predicted Total Area</th>
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33
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<th>46</th>
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<th>29</th>
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<th>29</th>
<th>54</th>
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Figures

**Figure 1.** Percent variable contribution of explanatory variables in each periodic Generalized Additive Mixed Model for the distribution of saiga antelopes in Betapak Dala. Temperature – Mean diurnal range of temperature during the survey period; INDVI- Integrated Normalized Difference Vegetation Index; Dist2water- Distance to nearest water source; Dist2town- Distance to nearest settlement; X,Y- Geographic coordinates of the groups; Year- Year of survey. Period I- 1986-1996; II- 1997-2002, III – 2003-2008.

**Figure 2.** Spring distribution for the Betpak Dala population of Kazakhstan in three different time-periods, based on the GAMM models. a) Period I 1986-1996; b) II 1997-2002 & c) III 2003- 2008. Black cells represent areas with high suitability (>0.5), dark grey cells- areas with medium suitability (0.2-0.5), and white with low suitability (<0.2).

**Figure 3.** Maps showing the Altyn Dala Conservation Initiative Boundary and protected areas (small polygons with black and white boundary) overlaid on modelled spring distribution of saiga for the past and current situation as well as the conservation success and failure scenarios (see Table 1 for details on scenarios and Figure S6 for all other scenarios). Black cells show the predicted high suitability, grey- medium and white cells the low suitability areas for saiga.

**Figure 4.** Predictions of saiga spring density in Betpak Dala based on a) Period I model (healthy past population); b) Period III (current situation); c) a scenario representing conservation success, in which the population recovers and group sizes get larger, with reduced disturbance but the climatic changes still occur (T+N-D-G+); and d) a scenario representing conservation failure, in which disturbance increases and the population does not grow (T+N-D+). Refer to Table 1 for details on scenarios.
Figure 1. Singh & Milner-Gulland
Figure 2. Singh & Milner-Gulland
Figure 3. Singh & Milner-Gulland
Figure 4. Singh & Milner-Gulland