Saiga antelope calving site selection is increasingly driven by human disturbance

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ABSTRACT

Many terrestrial mammalian species aggregate to give birth. Such aggregations are likely to be a response to changing resource and water availability, for predator swamping and avoidance of disturbance. The critically endangered saiga antelope (*Saiga tatarica*) is one such species. We analysed spatio-temporal locations of saiga calving aggregations in Kazakhstan over the last four decades obtained from aerial and ground surveys, to identify the factors determining the selection of calving sites within the species' range as well as any changes in these locations over time. Generalized mixed models were employed in a use – availability framework to assess the factors distinguishing calving from random sites and predict suitable areas for calving. Saigas selected sites, with lower than average productivity and low year to year variability in productivity, at an intermediate distance from water sources, and away from human settlements. A significant change in calving locations was observed during the last decade, with calving areas occurring further north and further away from settlements than previously. The results demonstrate that the choice of calving areas is largely driven by environmental factors. However, disturbance also has a significant impact on calving site selection and in recent decades, its influence overrides that of environmental factors. This increase in the influence of disturbance coincides with a precipitous decline in saiga numbers due to poaching, as well as substantial reductions in the intensity of land use for livestock grazing following the breakup of the Soviet Union. Predictive models based on such studies can improve species conservation by guiding the stratification of sampling for effective monitoring and deployment of rangers to protect the females at this critical time.

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1. Introduction

The reproductive success of female ungulates is often limited by severe environmental constraints on their abilities to conceive, gestate, lactate, and rear offspring (Rachlow and Bowyer, 1991; Gaillard et al., 2000; Tveraa et al., 2007; Bårdsen et al., 2008). In highly seasonal environments, where calving is synchronized with abundance of high-quality food, nutritional requirements of nursing females and risk of predation on their young reach a maximum during and shortly after parturition (Bowyer et al., 1998a,b; Rachlow and Bowyer, 1998). Calving site selection is important in determining the reproductive success of ungulate females and is generally a trade-off between maximizing energy gain by selecting high quality habitats and protecting the young against predators (Bowyer et al., 1998b; Kohlmann et al., 1996; Rachlow and Bowyer, 1998). For instance, female ungulates living in open environments tend to aggregate in large numbers to give birth, which is likely to be a predator swamping strategy (Milner-Gulland, 2001).

The saiga antelope (*Saiga tatarica*), is a long distance migratory species of the semi-deserts and steppes of Central Asia, in which females form large aggregations to give birth in spring, during their annual migrations to the summer ranges (Fadeev and Sludskii, 1982; Bekenov et al., 1998). The saiga's life history is characterized by aggregative calving behaviour and displays early female reproductive maturity (8 months), unusually large neonates relative to female body size, frequent twinning, long reproductive life (up to 12 years) and female-biased sex ratios (Bekenov et al., 1998; Kühl et al., 2007). The species is also critically endangered, having suffered a >90% population decline within a decade, due to poaching following the collapse of the Soviet Union (Milner-Gulland et al., 2001; Kühl et al., 2009a). The birth period is a particularly vulnerable time in their life history, during which the species is highly sensitive to human disturbance, to the extent that in recent years aggregations have failed to form in some populations (Fry, 2004). For this reason, the identification and protection of birth areas is a high priority for saiga conservation (Convention on Migratory Species, 2006).

Calving takes place between late April and early June (depending on the population), with mass calving occurring over

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a short period (3–8 days, Fadeev and Sludskii, 1982), after which the females move off to continue their migration. Observations suggest that the maximum potential size and location of a saiga aggregation are likely to be determined by the quality of the forage and water supplies available in an area, and that these may vary from year to year according to the climate (Iu.A. Grachev, pers. obs; Bekenov et al., 1998). In other species, calving moose (*Alces alces gigas*) select sites safe from predators as opposed to sites with higher forage and nutritional reward (Bowyer et al., 1999), whereas caribou (*Rangifer tarandus*) females disperse over large areas distancing themselves from the other females to reduce the risk of predation (Fuller and Keith, 1981; Stuart-Smith et al., 1997; Rettie and Messier, 2001). In the Serengeti, wildebeest (*Connochaetes taurinus*) females aggregate in large numbers during calving in response to predation risk from hyenas (Estes, 1976).

Monitoring of females and calves within the birth areas may be a good predictor of general population trends. Kühl et al. (2009b) suggested the use of a novel non-invasive technique of survey transects during the calving aggregation to estimate twinning rates and hence female age structure and population productivity. However, a primary difficulty encountered in carrying out such surveys is locating the calving aggregations when their locations are highly variable from year to year. With little information on calving locations and their annual variation, it is difficult to plan protection and monitoring strategies effectively. A predictive model identifying the calving aggregation sites may reduce the difficulties in finding such sites, when sampling is stratified based on these models. Knowledge of likely locations of calving grounds can also enable more efficient allocation of law enforcement and protection effort. Large aggregations have become extremely rare in recent times and this means that conservation planning is based on minimal, and potentially biased, information. The 'decision rule' currently followed for saiga population and calving aggregations surveys is the identification of current year survey areas on the basis of the previous year's sightings (Iu.A. Grachev pers obs). This creates a bias of uneven distribution of survey effort and a large part of the saiga range remaining un-surveyed. Improved understanding of calving locations based on iterative habitat use modelling may allow more precise prediction of saiga distributions and help to focus future surveys in un-surveyed areas, as well as improving survey efficiency (Singh et al., 2009).

Considering these conservation objectives and using a long-term dataset to provide empirical backing for our results, we identify the factors affecting calving site selection by saiga antelopes, assess differences in calving locations among the populations, identify any changes in calving site distribution during the last four decades and build a predictive model for calving site selection to inform conservation planning. We test three hypotheses concerning the factors determining calving site selection, related to *productivity, water availability and human disturbance*.

1.1. Productivity hypothesis

We predict that, over the broad spatio-temporal scale of the saiga's annual range, calving aggregations should coincide with the timing of peaks in productivity as observed in other ungulate species (Lenarz, 1979; Berger, 1992; Loe et al., 2005; Pettorelli et al., 2006). If higher forage productivity determines calving site selection, calving sites should have higher average productivity compared to random sites within the spring habitat. However, if the calving sites are determined by variability of productivity of a site, sites with lower variability of productivity should be selected to ensure consistent forage availability every year.

1.2. Water availability

As availability of water is essential for lactating females during the calving period, calving sites should be located closer to water than the random sites.

1.3. Human disturbance

If human disturbance affects calving site selection, sites should be located farther away from settlements compared to random sites and calving sites in high disturbance years (since the onset of high poaching levels in the 1990s, following the collapse of the Soviet Union) should be located further from settlements as compared to those in low disturbance years.

2. Materials and methods

2.1. Study area

The Republic of Kazakhstan, currently contains 75% of the saiga population. It is generally flat, covered by treeless steppe, semi-desert and desert vegetation except in the farthest north and south. It is characterized by hot summers and severe winters, during which the temperature may drop as low as −40 °C. In the south and east of the country are the Tien Shan and Altai mountain ranges, rising to 7000 and 4000 m, respectively. Vegetation zones occur in a latitudinal gradient (Fig. 1). The northernmost steppe zone is followed by semi-desert and desert zones with annual precipitation of around 300 mm, 200–250 mm and <250 mm, respectively. The saigas inhabit all three vegetation zones on a seasonal basis (Bannikov et al., 1961; Bekenov et al., 1998; Fadeev and Sludskii, 1982). They undertake annual spring migrations to the summer grounds in the north and northwest and return autumn migrations to their winter ranges to the south and southeast. These migrations are probably driven by the need for new green pastures in the spring (March–May) and by the presence of deep snow starting in autumn (September–October, Bekenov et al., 1998; Singh et al., in press).

The saiga population in Kazakhstan is divided into three populations named Betpak dala, Ustiurt and Ural after their regions (Fig. 1). The period, route, distance and speed of migration differ from year to year and among the three populations, depending on climatic conditions, the condition of pastures, the number of watering places, the degree of disturbance experienced by the animals and various artificial obstacles on migration routes. The calving areas are located on the course of the spring migration, mostly in the desert and semi-desert areas and in areas of relatively even terrain and less commonly, in hilly sands stabilized by vegetation. Prior to the 1990s, the typical size of a large aggregation varied from 50,000–150,000 animals, but has declined significantly in recent decades (Milner-Gulland, 2001; Kühl et al., 2009b). In these aggregations, animals are distributed relatively evenly across the calving areas, at an average density of five to seven calves per hectare (Fadeev and Sludskii, 1982; Kühl, 2007). From region to region, the area of the saiga's calving grounds varies from 100 to 9000 km^2 (usually 150–900 km^2; Bekenov et al., 1998). Calves remain hidden for the first 2 days. At the age of 4–5 days, the calves move with their mothers to the periphery of the birth area, and at 8–10 days, they move off to the summer pastures (Bannikov et al., 1961). The main predator of saigas is the wolf (*Canis lupus*), which particularly takes newborn saigas, though dogs may also kill saigas during calving, and eagles (*Aquila chrysaetos*) kill newborn calves.

2.2. Data sources

The calving site locations were acquired from the aerial and ground survey reports of the Institute of Zoology, Kazakhstan, for
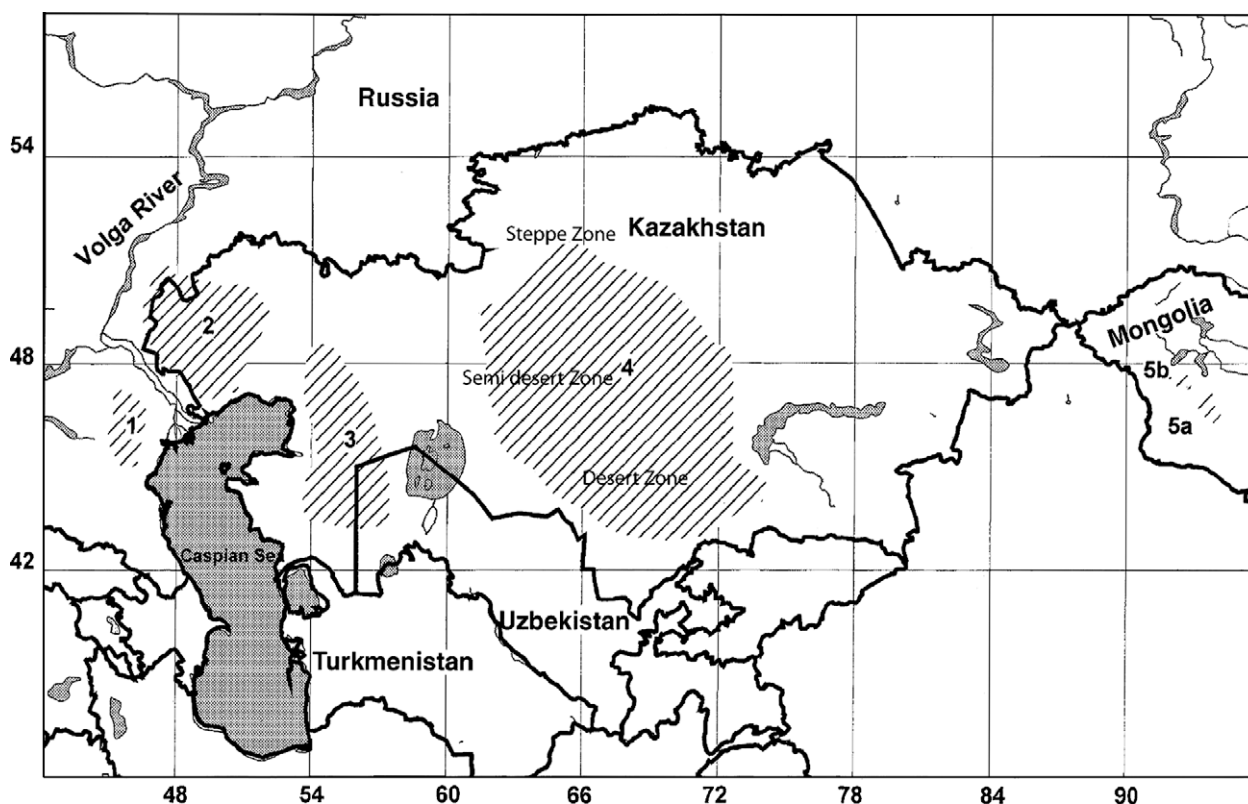
Fig. 1. Population ranges of existing saiga (*Saiga tatarica*) populations: (1). pre-caspian (Russia), which is not considered in this paper; (2) Ural (Kazakhstan); (3) Ustiurt (Kazakhstan); (4) Betpak dala (Kazakhstan); (5a and b) Mongolia, (the sub-species *S. t. mongolica*, also not considered). Figure modified from Milner-Gulland et al. (2001).

the time period 1970–2008, which contain information on dates of survey (mainly April–May), areas surveyed and population-specific distributions for the three main populations. The survey team flies aerial transects (Sample transect paths – Appendix A) over the areas of highest saiga density, as determined from local and expert knowledge, aiming to cover 20% of the area. A population estimate is extrapolated by multiplying the number seen by the coverage and the size of the area of saiga concentration, calculated by drawing a line around the observations and counting grid squares within that line. There is no measure of error. The observations consist of the estimated size and approximate location of each group seen. This survey technique was developed during Soviet times, and hence does not follow standard Western protocols (e.g. Norton-Griffiths, 1978; Buckland et al., 2001). There is substantial potential for error and bias including unsystematic coverage of the survey area and poor practice when flying, introducing further, largely unquantifiable error and bias (Norton-Griffiths and McConville, 2007). These aerial surveys are complemented with intensive ground surveys during spring with the primary aim of identifying calving areas and marking calves (unpublished data from survey reports, Institute of Zoology).

We transferred the most reliable observations from these aerial and ground surveys as point locations into a geographic information system (GIS). The locations from aerial surveys were generally plotted on the topographic maps directly during the surveys and the ones from ground surveys were either described in the survey reports as the distance to nearest landmark/settlement in a specific direction or plotted on topographical maps. GPS was not available during these surveys. Since the observations were also irregular in time and lacked a specific systematic sampling methodology, we pooled all the available locations during the calving period to identify the general calving range in Kazakhstan, grouped into decades (Appendix B). Decade of observation and population were included

as factors in the analyses. We pooled the years into decades as the data were not consistent in every year, with not all suitable calving areas being sampled, leading to an unequal sampling effort and non-coverage of all potential calving sites (McConville et al., 2009). Hence it is difficult to assume that year reasonably represents changes in density. So decade of observation was used as a proxy for saiga density, with early decades (1970s–1980s) representing high densities and later decades, low densities (1990s–2000s). In total, we recorded 213 calving locations (Betpak dala – 128, Ural – 36 and Ustiurt – 47) over the study period. There were 121 calving locations recorded for 1970–1979, 50 for 1980–1989, 37 for 1990–1999 and 26 for 2000–2006, respectively (Appendix B).

2.3. Variables

For estimating the long term average forage productivity of the saiga range, we acquired Normalized Difference Vegetation Index scenes (NDVI) from the 15-day GIMMS (Global Inventory Modelling and Mapping Studies) dataset (8×8 km spatial resolution – ftp://ftp.glcf.umiacs.umd.edu/glcf/GIMMS/Geographic/; Pinzon et al., 2005; Tucker et al., 2005) for the part of the time period corresponding to the calving site data (1981–2006). NDVI data were then resampled into 1×1-degree grid system. Using these images, we also estimated the coefficient of variation (CV) of NDVI for each pixel in the area during the spring months to obtain a measure of long term variability in NDVI.

The distance to the nearest water areas and settlements were estimated for each calving location based on maps acquired from 'Biogeomencer project' (http://www.biogeomancer.org/) for water areas and 'Global database on Administrative areas' (http://bio-geo.berkeley.edu/gadm/) for settlements. The distance to the nearest settlement in the database was regarded as an indicator of the

level of disturbance due to poaching pressure. We hypothesise that in more populous and better connected areas, recent increases in poaching pressure are likely to have been more severe (Kühl et al., 2009a). All the settlements in our database were established by 1970, and following the collapse of the Soviet Union, population growth has mainly occurred in larger cities and through abandonment of isolated farms rather than through changes in the small-medium sized towns and villages characteristic of the saiga range (Propastin and Kappas, 2008). In our database, we include all standing water, whether permanent or seasonal, because the calving period is a time of high water availability, when seasonal water bodies are filled. In addition to the vegetation and climatic variables, we also recorded the geographical coordinates for each calving location and projected then into Universal Transverse Mercator (UTM) projection.

3. Analyses

3.1. General characteristics of the calving locations

All the calving site observations were first pooled to identify the main factors affecting calving site selection on the population scale. Random sites for comparison were taken from within a polygon surrounding the recorded range of the saiga antelope in the spring period (March–May). The boundaries of the polygon were defined based on the total area surveyed during the annual spring population and distribution surveys conducted by the Institute of Zoology of Kazakhstan (Appendix A). The values for average and CV of spring NDVI were extracted for each site using the Point Intersect tool, in the Hawth's Tools extension of ArcGIS 9.2 (ESRI). Distances of sites from the nearest water source and settlements were estimated in ArcGIS 9.2 using the analysis toolbox's 'near' function in the proximity tool. We used these variables in a use-availability framework to identify the differences between the calving ($n = 213$) and random sites ($n = 301$; Manly et al., 2002).

To find the appropriate combination of variables distinguishing the used from random sites we adopted generalized linear mixed models with use as the binomial response variable and average spring precipitation and CV of spring precipitation, average spring NDVI and CV of spring NDVI, latitude, distance to water and distance to settlements as fixed effects. Second order terms were included for distance to water due to the non-linearity. Decade (1970s, 1980s, 1990s and 2000s) and populations (Betpak Dala, Ustiurt and Ural), were also included as fixed effects. To account for the variability explained by the sites, calving location ID was treated as a random effect. All the variables were scaled before use by dividing the centered columns of each variable by their root-mean-square and were assessed for correlations using a correlation matrix and the variance inflation factor (VIF) of each variable (Appendix C). The VIF shows how much the variance of the coefficient estimate is being inflated by multi-collinearity and a value exceeding 5 is considered as an evidence of multi-collinearity. None of the variables considered showed a high VIF, hence they were included in the same model. Model selection was performed using Akaike's information Criterion (AIC; Burnham and Anderson, 2002). Models containing polynomial term without the linear term of a variable were discarded. All the statistical analysis was done in R 2.7.2 and R libraries 'lme4' and 'nlme' were used for running the mixed models (R Development Core Team, 2008).

3.2. Predicting calving site usage and model validation

We used the model results to generate spatial predictions for each decade using the significant variables and formulating a sep-arate model for each decade. The variable contribution for the selected decadal models was estimated using the predictive contribution coefficient (Ratner, 2003). To evaluate the models we used the K-fold cross validation (Boyce et al., 2002; Elith et al., 2006; Johnson et al., 2006). We allocated the data randomly into four cross-validation groups for each decade, based on the method of Fielding and Bell (1997). To determine bin size and number, we divided predictions into equal interval bins scaled between the minimum and maximum scores. We then divided the bins into 6 partitions based on histogram-equalized stretches that base bin levels on frequency of occurrence (Lillesand and Kiefer, 1994). A good predictive model is expected to have an increasing area-adjusted frequency of calving sites in higher-ranked bins and hence a significant and positive r_s. Changes in the predicted area of usable habitat over time were estimated by measuring the area falling into habitat use classes defined as low (0–0.2), medium (0.2–0.5) and high (0.5–0.99) predicted use, based on the fitted probabilities from the full models (Liu et al., 2005; Johnson et al., 2006; Freeman and Moisen, 2008). We defined these three classes using the model results (Boyce et al., 2002; Hirzel et al., 2006; Johnson et al., 2006) in order to achieve a compromise between the range of usability and the size of the areas of each habitat use class (Singh et al., 2009). The percentage area falling under each class was estimated based upon the maximum extent of saiga sightings in the spring period.

4. Results

Productivity, water availability and human disturbance were all important in determining calving site selection by the saiga antelope.
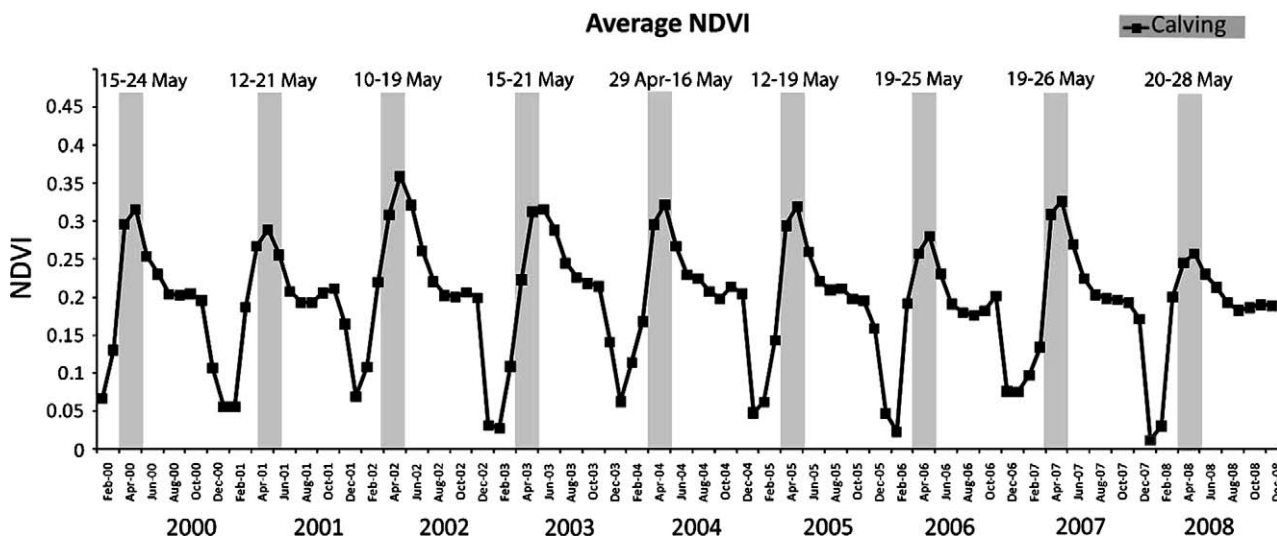
4.1. Productivity

In the time period for which both the dates of calving and NDVI were available, calving period coincided with the occurrence of peaks in Normalized Difference Vegetation Index (NDVI) over the year (supporting the *productivity hypothesis*; Fig. 2). However, the model results suggested that within this period of peak productivity, the calving sites selected had lower average NDVI than the random sites, contrary to our predictions (top model Est. ± Std.Error: -0.25 ± 0.09), but also lower variability of NDVI (-0.43 ± 0.12) in line with our predictions (Table 1).

4.2. Water availability

The distance to water and its second order polynomial, emerged as important variables indicating that the calving sites were at intermediate distance from water compared to the random sites in the spring range (distance to water: -0.17 ± 0.12; distance to water^2: -0.08 ± 0.01, Table 1). These results contradict our predictions that calving site should be closer to water sources.

4.3. Human disturbance

With reference to the human disturbance hypothesis, the calving sites were away from settlements (distance to towns: 0.52 ± 0.10). Latitude, population and the interactions between decade and both latitude and distance to settlements were also significant (Table 1). The trend in interaction between the decades and distance to settlements indicates that calving sites were significantly further away from settlements in the 2000s than previously (coefficients: 1970s: -0.1 ± 0.08, 1980s: 0.09 ± 0.01, 1900s: 0.21 ± 0.03, 2000s: 0.56 ± 0.09). The significant interaction between decade and latitude indicates that during the last decade there has

Fig. 2. Monthly and annual trends in primary productivity (measured as NDVI) in the saiga's spring ranges in Kazakhstan over the last decade, and the observed dates of calving averaged for the three Kazakhstan populations, (shaded). Numbers above the bars represent the dates in May of the calving period, as recorded in the Institute of Zoology's annual reports.

Table 1

Comparisons of changes in AIC (ΔAIC) and AIC weights (*w*) for the 10 best models for calving site selection by saiga antelopes in Kazakhstan. Values are parameter estimates (coefficients) for the variables included in the models. An empty cell indicates the variable is not included in the model. Variable importance is indicated in bold in the last row of the model set. CVNDVI – coefficient of variation of Normalized Difference Vegetation Index; dist2town – distance from nearest human settlement; dist2water – distance from the nearest water source; dist2water2 – quadratic term for the dist2water; NDVI – average Normalized Difference Vegetation Index; pop – population, *x* – latitude, *k* – number of variables included in the model, AIC – Akaike's information criterion, Dev. – deviance.

(Int.)	CVNDVI	Dist2town	Dist2water	Dist2water2	NDVI	Pop	*x*	Dist2town Decade	Decade:*x*	*k*	Dev.	ΔAIC	*w*
−0.23	−0.26	0.52	−0.19	−0.08	−0.37	0.14	0.01	0.15	0.22	9	647.99	0.00	0.43
−0.15	−0.25	0.50	−0.05	−0.01	−0.38	0.15		0.15	0.22	8	646.36	0.37	0.30
0.22	−0.26	0.54	−0.18	−0.06	−0.36	0.13	0.02	0.14	0.23	9	647.56	1.57	0.09
−0.26	−0.28	0.49	−0.17	−0.08	−0.38	0.14		0.15	0.30	8	651.90	1.91	0.06
0.31	−0.26	0.53	−0.04	−0.08	−0.37		0.03	0.13	0.33	8	645.92	1.93	0.06
0.38	−0.28	0.53	−0.06	−0.01	−0.37	0.11	0.01	0.12	0.32	9	651.03	3.04	0.02
−0.09	−0.29	0.50	−0.04	−0.10	−0.35	0.12		0.15		7	651.62	3.63	0.01
−0.18		0.51	−0.20		−0.33				0.14	4	653.69	3.70	0.01
0.34		0.52	−0.03	−0.10	−0.34	0.13	0.02		0.14	7	651.23	5.25	0.00
0.23		0.54	−0.20		−0.33	0.17	0.02		0.15	6	653.33	5.34	0.00
	0.98	1.00	1.00	0.99	1.00	0.93	0.61	0.98	0.99				

been an overall change in the general locations of calving sites with sites shifting significantly further north (coefficients: 1970s: 0.51 ± 0.19, 1980s: 0.52 ± 0.11, 1900s: 0.32 ± 0.06, 2000s: 0.20 ± 0.01). The variable "population" is also significant, suggesting geographical differences between the three populations, with the most westerly population (Ustiurt) most different from the baseline population (Betpak dala), which is around 1000 km to the east. The random effect of location, estimated through the maximum likelihood method, only explained 3% of the variance.

4.4. Predictive modelling and validation

The importance of the explanatory variables within the decadal models varied by decade (Fig. 3, Model Coefficients – Appendix D). NDVI was the variable that contributed the most explanatory power to the models during all four decades, however its relative importance decreased over time after the 1980s. The importance of distance to settlements increased with each decade, reaching a maximum during 2000–2008, whereas that explained by the CV of NDVI was generally variable since the 1970s. Also, the second order polynomial of distance to water contributed more during
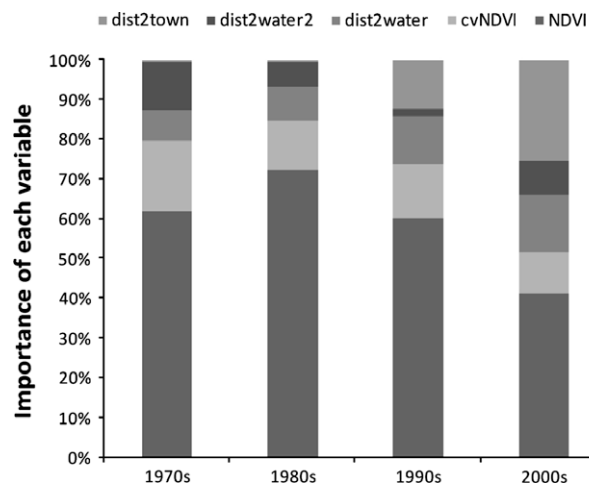
Fig. 3. Relative importance of the variables in the calving site selection models for each considered decade (1970s–2000s). NDVI – Normalized Difference Vegetation Index; CVNDVI – CV of NDVI (%); dist2towns – distance from nearest settlements (km); dist2water – distance from the nearest water source (km); dist2water² – square of the distance to the nearest water source.
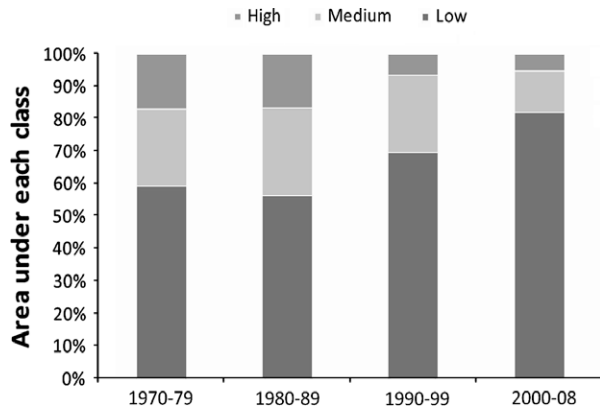
Fig. 4. Percentage changes in usable calving habitat over time based on the mixed models. Habitat is divided into low (0–0.2), medium (0.2–0.5) and high (0.5–0.99) usability based on the fitted probabilities from the full models.

the last two decades than earlier. There was around a 35% decline in the habitat area predicted to be well used by saigas during the last two decades (Fig. 4). The cross validation for each model by decade gave an average Spearman rank correlation $r_s > 0.78$ between bin ranks and the area-adjusted frequencies, with an average P value of <0.03 (Appendix E), indicating good model performance.

5. Discussion

As predicted, the calving period of the saiga antelope coincides with the peak in vegetation productivity in the desert and semi-desert areas of Kazakhstan. Female ungulates living in highly seasonal environments increase their reproductive success by synchronising their calving period with periods of high forage abundance (Sand, 1996; Sæther et al., 1996; Loe et al., 2005; Pettorelli et al., 2006), and saiga females also follow this strategy.

During the calving period, in the spring range it is generally green everywhere, hence it is not surprising that *productivity hypothesis* for calving site choice within the spring range is refuted. In such a situation, it may not be especially beneficial to select sites with higher average forage abundance. Instead, the observed selection of sites with lower NDVI but also lower year to year variation in NDVI may signify the importance of places where saiga females can consistently find productive habitat rather than those where high productivity may occur but is not guaranteed. In addition other finer scale factors may also play a role in the selection of calving sites. For example, females may select sites with cover or sheltered areas where the wind is less extreme and flat plains where predators can be easily sighted. Bekenov et al. (1998) suggested that saigas typically calve in areas containing *Artemisia, Salsola, Festuca sulcata, Stipa*, and shrubs of *Haloxylon, Salsola arbuscula* and *Spiraea hypericifolia*; on the bare edges of salt pans and salt marshes which may provide depressions for the calves to hide in. However lack of information on the distribution of vegetation communities limits us from speculating further about the fine-scale drivers of calving site selection.

The calving sites were located neither too close, nor too far from the nearest source of water (*water availability* hypothesis), which could imply a trade-off between predation, disease or disturbance risk and water requirements during parturition (Bowyer et al., 1999; Milner-Gulland et al., 2001; Morgan et al., 2005). There has been a reduction in the availability of artificial water sources since the collapse of the Soviet Union, due to lack of maintenance (Kerven et al., 2006). Hence in recent years, livestock have become more dependent on natural standing water, which may explain the increasing role of water in determining calving site distributions in recent decades.

Saigas are known to be affected by disturbance (Bekenov et al., 1998), which was demonstrated here through the calving sites being located away from settlements (*human disturbance hypothesis*). This response is probably due to intense poaching around human settlements since the collapse of the Soviet Union (Kühl et al., 2009a), as well as land use changes and infrastructural activity as herds were concentrated around settlements (Kerven et al., 2006). Furthermore, rapid infrastructural and economic development has been taking place in recent decades in Kazakhstan which includes road construction, pipelines, mining and other activities which potentially threaten saiga habitat (Human development report, United Nations Development Programme, 2002). These trends are visible through the interaction between decade and distance to settlements, whereby calving sites in recent decades are observed to be moving further away from settlements. The non-significant, result observed during the 1990s of calving sites being located closer to settlements may be related to the transient effects of the aftermath of the breakup of the Soviet Union, during which the population size of many settlements declined rapidly. However, the pooling of yearly observations into decades may also hide the year to year variation in the selection of calving sites which may bring about such observations.

The interaction between decade and latitude, indicating a shift in calving sites towards the north during the last decade, could be due to factors such as changing climate. Bekenov et al. (1998) reported that calving areas of the Ural population had moved north during the 1990s due to milder winters and little snow. Climate change models predict an increase in winter precipitation and a decrease in summer precipitation in the desert areas of Kazakhstan (IPCC, 2007). Such changes have the potential to modify the entire migratory behaviour of saiga as well as produce severe limitations to population growth through increased snow in winter and lower productivity in summer. Also, in such a scenario, changes in precipitation and related variables such as NDVI and availability of water are likely to affect calving site selection. Hence changes in monthly and seasonal precipitation and NDVI over time and at finer scales need further investigation.

The calving areas of all three populations occur at different latitudes and longitudes. Not only do the environmental conditions vary at these locations, but the threats and disturbance factors are also different. Such variance in conditions in calving grounds may well bring about variation between populations in the survival and fitness of the newborn calves. Calving aggregations are reported to be declining in size in recent decades with many fewer of the large calving aggregations being observed, especially in the Ustiurt population (Fry, 2004). The Institute of Zoology survey reports testify to significant declines in observations of calving aggregations for all three populations (Institute of Zoology, Kazakhstan, unpublished data). These declines are attributed to a general decline in saiga population size (Milner-Gulland et al., 2001) and increased poaching and human disturbance (Kühl et al., 2009a). Game theoretic modelling suggests that at high levels of disturbance it is no longer advantageous for females to aggregate (Milner-Gulland, 2001). Given that our models suggest an increasingly strong effect of human disturbance on the location of aggregations, such factors may also explain the reduction in the number and size of calving aggregations in Kazakhstan.

Other factors not considered here may also have important implications for the selection of calving sites by females. Over the last four decades, it is likely that population densities have declined in parallel with the reduction in absolute numbers. This could have greatly affected the choice of calving areas by saiga

females. Density is known to affect habitat selection in several gregarious species (Clutton-Brock et al., 1987; Kie and Bowyer, 1999; Hebblewhite et al., 2002). Although the data from aerial surveys suggest changes in densities, the changes are not robustly quantified, as the surveys record only group size and approximate location of sightings (McConville et al., 2009). The issues with our dataset, such as lack of absences and coarse resolution, preclude modelling of year-by-year changes in density and habitat use, hence the choice of a decadal scale for temporal analysis. However on this scale, changes in density are confounded with decade. Hence any effects of density on habitat use are bundled within the decadal changes in variable importance (Fig. 3).

A further potentially important influence on saiga habitat use could be changes in predator density or behaviour, in this case wolves. The calving females and new born calves may no longer be aggregated in sufficient numbers to saturate the predators (Milner-Gulland, 2001). Changes in prey densities are known to affect the predator's functional and numerical responses (Messier, 1994; Hebblewhite et al., 2002; Hinkes et al., 2005). No scientific observations on wolf habitat selection, densities or predation rates are available for the study area, preventing us from making inferences about the effect of this factor.

We have shown that multiple factors explain calving site selection by saiga antelopes. Saiga females probably minimize risk to the young by selecting sites away from water bodies and settlements. More fine scale and detailed studies on saiga behaviour during the calving period are nonetheless required to understand the actual factors determining the location and size of calving aggregations. Also, daily activity and ranging patterns of females need to be assessed. Although our analysis brings out key factors affecting calving site selection, the dataset has important limitations. The calving site surveys were not systematic and consistent over time. Since calving aggregations are spread over large areas, considering a point location as a calving site may not be a very precise representative of the calving site selected. The dispersion of watering places as well as particular vegetation communities may vary in a large calving site and hence considering one point as the calving site may be misleading.

The predictive model for the most recent decade is intended as a tool to stratify future sampling effort in identifying calving sites (Appendix F). Significant changes were observed in the availability of usable habitat, and in the importance of each variable in defining that habitat, over the last four decades. We have found evidence for changes in calving habitat use linked to human disturbance. Nevertheless, a more robust model of the geographic distribution of calving site selection will need to include an explicit consideration of the functional relationship between predictors and the behaviour of saiga herds, rather than a correlative methodology such as the one used here. These model results can still be improved greatly by incorporating new observations into the datasets as they are encountered, so that the results presented here can be used as a tool for stratifying sampling in future surveys of calving sites and help to reduce both survey effort and bias by enhancing model precision (e.g. Singh et al., 2009). This method thus has potential both for increasing detection of calving sites for research purposes and for prioritizing areas for conservation at a time when this critically endangered species is particularly vulnerable.
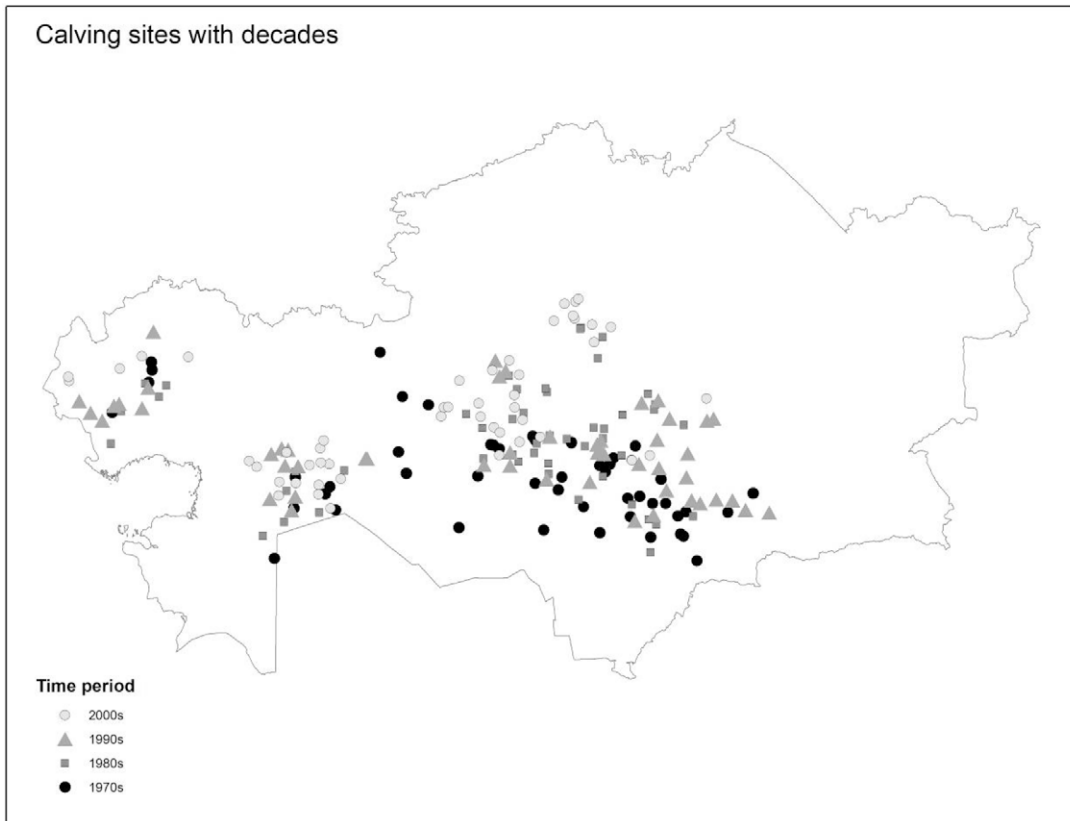
Acknowledgements

Appendix A

A sample map of the areas covered in the spring aerial surveys in Kazakhstan. The map presented is for 1983.
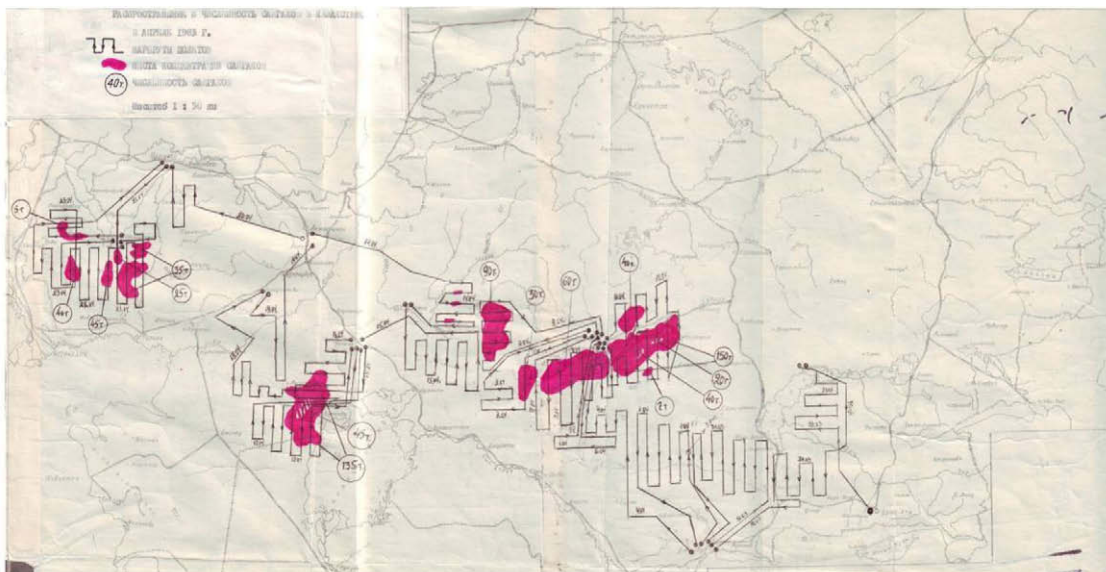
Appendix B

Locations of calving sites by decade in Kazakhstan.

Appendix C

Correlations between the variables used to assess the calving site selection (in 1970–2008) by saiga antelope (*Saiga tatarica tatarica*) in Kazakhstan. NDVI – Normalized Difference Vegetation Index; CVNDVI – coefficient of variation of NDVI; dist2water – distance from the nearest water source; dist2town – distance from nearest settlement. Values in bold are significant at $P < 0.001$. VIF – variance inflation factor for each variable.

	NDVI	Dist2water	Dist2town	CVNDVI	VIF
NDVI	1.00				1.85
Dist2water	0.03	1.00			1.00
Dist2town	−0.23	0.05	1.00		1.13
CVNDVI	−0.26	0.02	0.18	1.00	1.13

Appendix E

Spearman rank correlations between the area-adjusted frequencies and bin ranks. Frequency values for individual cross validation sets.

| Training sets Group	1970s r_s	P value	1980s r_s	p value	1990s r_s	P value	2000s r_s	p value
1	0.89	0.030	0.99	0.0028	0.79	0.045	0.68	0.048
2	0.99	0.017	0.94	0.017	0.65	0.047	0.92	0.001
3	0.98	0.003	0.99	0.0028	0.86	0.038	0.84	0.002
4	0.88	0.033	0.94	0.017	0.99	0.001	0.78	0.041
5	0.82	0.038	0.83	0.058	0.70	0.039	0.98	0.001
6	0.93	0.001	0.78	0.040	0.69	0.049	0.66	0.042
Mean	0.92	0.020	0.92	0.023	0.78	0.037	0.81	0.023

Appendix D

The variable coefficients for each decadal model used for creating habitat suitability model for calving sites for saiga antelope.

	Intercept	NDVI	Dist2water	Dist2water2	Dist2town	CVNDVI
1970s	−0.298	−0.369	−0.157	−0.026	0.086	−0.256
1980s	−0.357	−0.472	−0.102	−0.097	0.121	−0.312
1990s	−0.312	−0.282	−0.089	−0.132	0.228	−0.323
2000s	−0.368	−0.357	−0.205	−0.154	0.511	−0.457

Appendix F

Predicted calving site usability in time, based on the mixed, where values <0.2 represent low, 0.2–0.5 = medium and >0.5 = high predicted use.
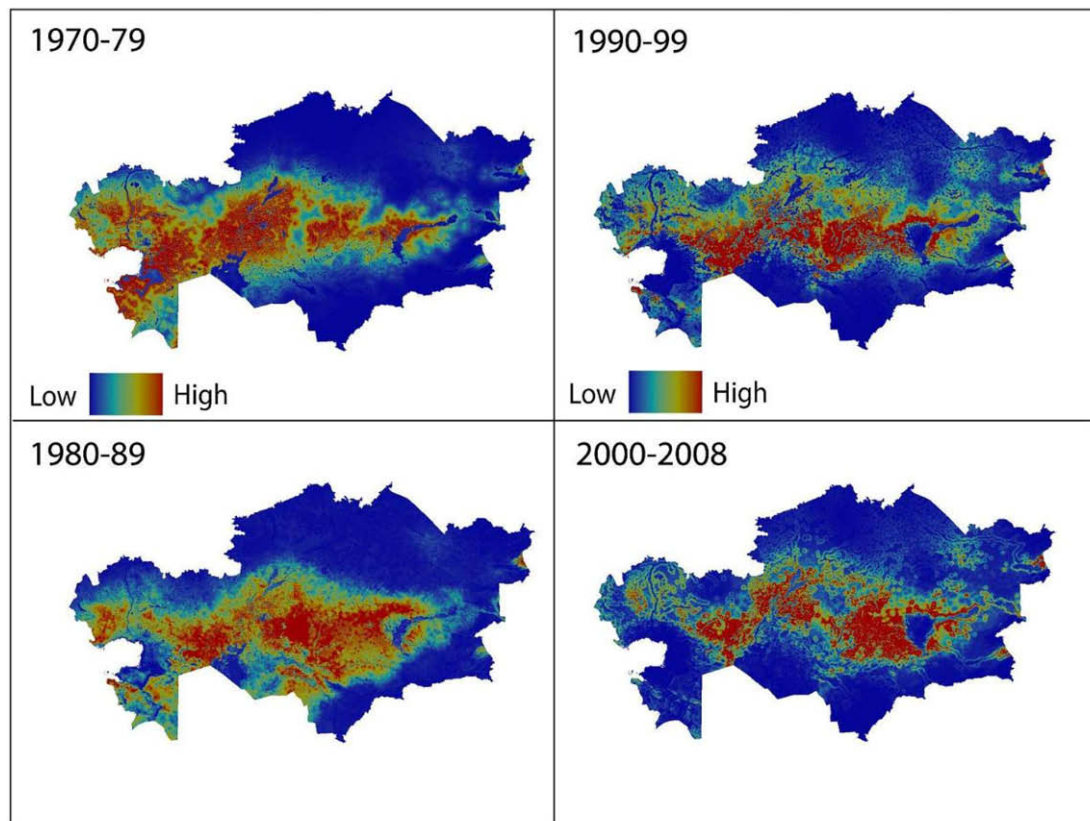
References

Bannikov, A.G., Zhirnov, L.V., Lebedeva, L.S., Fandeev, A.A., 1961. Biologiya saigaka [Biology of the saiga antelope]. Selskokhozyaistvennaya Literatura, Moscow.

Bårdsen, B.J., Fauchald, P., Tveraa, T., Langeland, K., Yoccoz, N.G., Ims, R.A., 2008. Experimental evidence for a risk sensitive life history allocation in a long-lived mammal. Ecology 89, 829–837.

Bekenov, A.B., Grachev, I.A., Milner-Gulland, E.J., 1998. The ecology and management of the Saiga antelope in Kazakhstan. Mammal Review 28, 1–52.

Berger, J., 1992. Facilitation of reproductive synchrony by gestation adjustment in gregarious mammals: a new hypothesis. Ecology 73, 323–329.

Bowyer, R.T., Kie, J.G., van Ballenberghe, V., 1998a. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? Journal of Mammalogy 79, 415–425.

Bowyer, R.T., van Ballenberghe, V., Kie, J.G., 1998b. Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. Journal of Mammalogy 79, 1332–1344.

Bowyer, R.T., van Ballenberghe, V., Kie, J.G., Maier, J.A.K., 1999. Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. Journal of Mammalogy 80, 1070–1083.

Boyce, M., Vernier, P., Nielsen, S., Schmiegelow, F., 2002. Evaluating resource selection functions. Ecological Modelling 157, 281–300.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to Distances: Estimating Abundance of Biological Populations. Oxford University Press, Oxford.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information – Theoretic Approach, second ed. Springer-Verlag.

Clutton-Brock, T.H., Iason, G.R., Guinness, F.E., 1987. Sexual segregation and density-related changes in habitat use in male and female red deer (*Cerrus elaphus*). Journal of Zoology 211, 275–289.

Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S., Richardson, K., Schachetti Pereira, R., Schapire, R.E., Soberón, J., Williams, S.E., Wisz, M., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.

Estes, R.D., 1976. The significance of breeding synchrony in the wildebeest. African Journal of Zoology 14, 135–152.

Fadeev, V.A., Sludskii, A.A., 1982. Saigak v Kazakhstane [The Saiga in Kazakhstan.] Alma-Ata, USSR, 160 pp.

Fielding, A.L., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24, 38–49.

Freeman, E.A., Moisen, G.C., 2008. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. Ecological Modelling 217, 48–58.

Fry, M., 2004. The status of the Saiga antelope in the Ustiurt region of western Kazakhstan. MSc Thesis, Imperial College London. <www.iccs.org.uk>.

Fuller, T.K., Keith, L.B., 1981. Woodland caribou population dynamics in north-eastern Alberta. Journal of Wildlife Management 45, 197–213.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., Toigo, C., 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31, 367–393.

Hebblewhite, M., Pletscher, D.H., Paquet, P.C., 2002. Elk population dynamics in areas with and without predation by recognizing wolves in Banff National Park, Alberta. Canadian Journal of Zoology 80, 789–799.

Hinkes, M.T., Collins, G.H., van Daele, L.J., Kovach, S.D., Aderman, A.R., Woolington, J.D., Seavoy, R.J., 2005. Influence of population growth on Caribou herd identity, calving ground fidelity and behaviour. Journal of Wildlife Management 69, 1147–1162.

Hirzel, A., Le Lay, G., Helfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling 199, 142–152.

IPCC – Intergovernmental Panel for Climate Change. 2007. Fourth Assessment Report on Climate Change. <http://www.ipcc.ch/ipccreports/assessments-reports.htm>.

Johnson, C.J., Nielsen, S.E., Merrill, M.E., McDonald, T.L., Boyce, M., 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70, 347–357.

Kerven, C., Alimaev, I., Behnke, R., Davidson, G., Smailov, A., Temirbekov, S., Wright, I.A., 2006. Fragmenting pastoral mobility: changing grazing patterns in post-Soviet Kazakstan. In: Bedunah, D. (Ed.), Rangelands of Central Asia: Transformations, Issues and Future Challenges. Rocky Mountain Research Station Serial. US Dept. of Agriculture, Fort Collins Colorado, USA.

Kie, J.G., Bowyer, R.T., 1999. Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. Journal of Mammalogy 80, 1004–1020.

Kohlmann, S.G., Müller, D.M., Alkon, P.U., 1996. Antipredator constraints on lactating Nubian ibexes. Journal of Mammalogy 77, 1122–1131.

Kühl, A., 2007. The Conservation Ecology of the Saiga Antelope. PhD Thesis, Imperial College London, London.

Kühl, A., Mysterud, A., Erdnenov, G.I., Lushchekina, A.A., Grachev, I. A., Bekenov, A.B., Milner-Gulland, E.J., 2007. The 'big spenders' of the steppe: sex-specific maternal allocation and twinning in the saiga antelope. In: Proceedings of the Royal Society B – Biological Sciences, vol. 274, pp. 1293–1299.

Kühl, A., Balinova, N., Bykova, E., Arylov, Y.N., Esipov, A., Lushchekina, A.A., Milner-Gulland, E.J., 2009a. The role of saiga poaching in rural communities: linkages between attitudes, socio-economic circumstances and behaviour. Biological Conservation 142, 1442–1449.

Kühl, A., Mysterud, A., Grachev, Iu.A., Bekenov, A.B., Ubushaev, B.S., Lushchekina, A.A., Milner-Gulland, E.J., 2009b. Monitoring population productivity in the saiga antelope. Animal Conservation 12, 355–363.

Lenarz, M., 1979. Social structure and reproductive strategy in desert bighorn sheep (Ovis canadensis mexicana). Journal of Mammalogy 60, 671–678.

Lillesand, T.M., Kiefer, R.W., 1994. Remote Sensing and Image Interpretation, third ed. Wiley, New York. p. 750.

Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385–393.

Loe, L., Bonenfant, C., Mysterud, A., Gaillard, J.M., Langvatn, R., Klein, F., Calenge, C., Ergon, T., Pettorelli, N., Stenseth, N.C., 2005. Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. Journal of Animal Ecology 74, 579–588.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Kluwer Academic Publishers, New York, USA.

McConville, A.J., Grachev, Iu.A., Keane, A., Coulson, T., Bekenov, A.B., Milner-Gulland, E.J., 2009. Reconstructing the observation process to correct for changing detection probability of a critically endangered species. Endangered Species Research 6, 231–237.

Messier, F., 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75, 478–488.

Milner-Gulland, E.J., 2001. A dynamic game model for the decision to join an aggregation. Ecological Modelling 145, 85–99.

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

Morgan, E.R., Shaikenov, B., Torgerson, P.R., Medley, G.F., Milner-Gulland, E.J., 2005. Helminths of saiga antelope in Kazakhstan: implications for conservation and livestock production. Journal of Wildlife Diseases 41, 148–161.

Norton-Griffiths, M., 1978. Counting Animals, second ed. African Wildlife Foundation, Nairobi.

Norton-Griffiths, M., McConville, A.J., 2007. Technical evaluation of the aerial survey programme for saiga antelope (Saiga tatarica) with recommendations for improvements. Final Report. ZGF-Project No. 1293/02 Saiga Schutz Kasachstan/Evaluation der Tierzahlungen. Frankfurt Zoological Society, Frankfurt.

Pettorelli, N., Gaillard, J.M., Mysterud, A., Duncan, P., Stenseth, N.C., Delorme, D., van Laere, G., Toïgo, C., Klein, F., 2006. Using a proxy of plant productivity (NDVI) to find key periods for animal performance. Oikos 112, 565–572.

Pinzon, J., Brown, M.E., Tucker, C.J., 2005. Satellite time series correction of orbital drift artifacts using empirical mode decomposition. In: Huang, N. (Ed.), Hilbert-Huang Transform: Introduction and Applications, pp. 167–186.

Propastin, P.A., Kappas, M., 2008. Linkages between the current climate change, the political change in Kazakhstan and trends in the photosynthetic activity of vegetation. In: Ehlers, M., Behnke, K., Gerstengarbe, F.W., Hillen, F., Koppers, L., Stroink, L., Wächter, J. (Eds.), Digital Earth Summit on Geoinformatics: Tools for Global Change Research. Wichman Verlag, Heidelberg, pp. 14–19.

R Development Core Team, 2008. A Language and Environment for Statistical Computing. R Foundation for statistical computing, Vienna.

Rachlow, J.L., Bowyer, R.T., 1991. Interannual variation in timing and synchrony of parturition in Dall's sheep. Journal of Mammalogy 72, 487–492.

Rachlow, J.L., Bowyer, R.T., 1998. Habitat selection by Dall's sheep (Ovis dalli): maternal trade-offs. Journal of Zoology (London) 245, 457–465.

Ratner, B., 2003. Statistical Modelling and Analysis for Database Marketing: Effective Techniques for Mining Big Data. Chapman & Hall, New York.

Rettie, W.J., Messier, F., 2001. Range use and movement rates of woodland caribou in Saskatchewan. Canadian Journal of Zoology 79, 1933–1940.

Sæther, B.-E., Andersen, R., Hjeljord, O., Heim, M., 1996. Ecological correlates of regional variation in life history of the moose Alces alces. Ecology 77, 1493–1500.

Sand, H., 1996. Life history patterns in female moose (Alces alces): the relationship between age, body size, fecundity and environmental conditions. Oecologia 106, 212–220.

Singh, N.J., Yoccoz, N.G., Bhatnagar, Y.V., Fox, J.L., 2009. Using habitat suitability models to sample rare species in high-altitude ecosystems: a case study with Tibetan argali. Biodiversity and Conservation. doi:10.1007/s10531-009-9615-5.

Singh, N.J., Grachev, I.A., Bekenov, A.B., Milner-Gulland, E.J., in press. Tracking greenery in central Asia – the migration of the saiga antelope. Diversity and Distributions.

Stuart-Smith, A.K., Bradshaw, C.J.A., Boutin, S., Hebert, D.M., Rippin, A.B., 1997. Woodland caribou relative to landscape patterns in north-eastern Alberta. Journal of Wildlife Management 61, 622–633.

Tucker, C.J., Pinzon, J.E., Brown, M.E., Slayback, D., Pak, E.W., Mahoney, R., Vermote, E., El Saleous, N., 2005. An extended AVHRR 8-km NDVI data set compatible with MODIS and SPOT vegetation NDVI data. International Journal of Remote Sensing 26, 4485–5598.

Tveraa, T., Fauchald, P., Yoccoz, N.G., Ims, R.A., Aanes, R., Høgda, K.A., 2007. What regulate and limit reindeer populations in Norway? Oikos 116, 706–715.