



Tracking greenery across a latitudinal gradient in central Asia – the migration of the saiga antelope

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ABSTRACT

Aim Long-distance migrations of terrestrial animals, driven by needs such as food, water and escaping predators and harsh climatic conditions, are widely known phenomena. The saiga antelope (*Saiga tatarica tatarica*) migrates over long distances in the semi-arid rangelands of Central Asia. Both the saiga's range and its populations have been severely affected by socio-political and land use changes over the last century, related to the formation and dissolution of the Soviet Union. We identified ecological drivers of saiga migration, compared four populations in terms of differences in the geographical characteristics of their ranges and the factors affecting habitat selection within the seasonal ranges.

Location Kazakhstan and pre-Caspian Russia.

Methods Using 40 years of direct observations, we tested for differences between the four saiga populations' ranges in terms of precipitation, seasonal productivity and topographical variables using discriminant analyses. We tested hypotheses concerning the drivers of migration to their seasonal ranges and assessed the impact of peak and average values and the predictability of drivers of habitat use within the seasonal ranges using logistic regressions.

Results Three of the four populations migrate in a similar way, following a latitudinal gradient driven by seasonal changes in productivity, which is closely related to broad-scale differences in precipitation. Intermediate productivity and its low interannual variability determine habitat selection within the seasonal ranges of all the populations.

Main conclusions Migration of all four populations is driven by productivity and precipitation. The migrations in Kazakhstan are still intact despite major recent disruption to the populations, whereas their status in the pre-Caspian region is unknown. All four populations are under severe threat from habitat loss, poaching, lack of protection and gaps in ecological knowledge. A better understanding of the drivers of saiga migration at multiple scales is a key step towards addressing these threats.

Keywords

Kazakhstan, long-distance migration, normalized difference vegetation index (NDVI), precipitation, Russia, *Saiga tatarica*.

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INTRODUCTION

Long-distance migrations (LDMs) of animals in search of food and water, tracking resources, escaping predation, parasites and harsh climatic conditions are spectacular phenomena widespread on all continents (Alerstam *et al.*, 2003; Bolger *et al.*, 2008). Recent interest in LDMs and their conservation has greatly enhanced our understanding and raised interest in

protection of the species undertaking these spectacular journeys (Thirgood *et al.*, 2004; Bolger *et al.*, 2008). Reviews of the status of migratory species in various continents indicate steep declines in their population numbers and available habitat, because of a range of factors including habitat loss, competition with domestic livestock, agriculture, construction of barriers that excludes animals from vegetation or water, hunting pressure and climate change (Serneels & Lambin,

2001; Berger, 2004; Fox *et al.*, 2009; Harris *et al.*, 2009). Only a few large terrestrial mammal species still migrate in aggregations comprising hundreds of thousands of animals. There is a lack of basic understanding of the ecology of these migrations, and some species, such as the saiga antelope (*Saiga tatarica*) and Tibetan antelope (*Pantholops hodgsonii*), even lack reports on their numbers, distances travelled, geographical routes and the ecological drivers of migration (Berger *et al.*, 2008; Harris *et al.*, 2009).

A variety of important ecological factors are known to drive and also limit these long-distance migrations. Seasonal peaks of resource abundance, specific nutrient demands, competition with resident individuals, escaping parasites, predators and extreme climate are among them (Jarman & Sinclair, 1979; Fryxell & Sinclair, 1988; Alerstam *et al.*, 2003). These factors vary geographically and by species. In highly seasonal environments, where the resource fluctuations are governed by broad-scale rainfall patterns, species seem to track these rainfall gradients or forage green-up indirectly governed by rainfall. These selection patterns may show interannual variations depending upon the rainfall and resource availability in a year. For example, wildebeest migrate within the Serengeti Mara Ecosystem in Africa, following a roughly circular pattern believed to be driven by rainfall and plant nutrient gradients (Talbot & Talbot, 1963; Jarman & Sinclair, 1979; Holdo *et al.*, 2009). Snowmelt across elevational gradients and the resulting vegetation growth drives the movements of bison (*Bison bison*), elk (*Cervus elaphus canadensis*) and caribou in North America (Fancy *et al.*, 1989; Toweill & Thomas, 2002).

The saiga antelope is a migratory species of the semi-arid rangelands of Central Asia, which travels hundreds of kilometres in large aggregations on a seasonal basis (Bekenov *et al.*, 1998; Milner-Gulland *et al.*, 2003). It has two subspecies, the nominate subspecies *S. t. tatarica* in Russia, Kazakhstan and Uzbekistan and the Mongolian saiga *S. t. mongolica* in Mongolia (Kholodova *et al.*, 2006). Saigas display 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 saiga is the only wild herbivore that occurs in significant numbers in the region. Their ecosystem lacks an elevational gradient and is relatively homogeneous in terms of landscape topography (Bekenov *et al.*, 1998). Nevertheless, high spatio-temporal variability in precipitation patterns in the saiga range does result in seasonal peaks and lows in resource abundance, which may drive their long-distance migration. The saiga was extensively hunted for its meat, horns and hide for centuries and overexploitation led to the species' near-extinction at the beginning of the 20th Century (Lushchekina & Struchkov, 2001). In the Soviet period, the state management authorities protected herds from disturbance and poaching, leading to population recovery (Bekenov *et al.*, 1998). However, extensive land use changes brought about by the 'virgin lands campaign' and livestock management during the Soviet period, modified the natural rangelands in the saiga range (Medvedev, 1987; Kerven *et al.*,

2006), and since the collapse of the Soviet Union in 1991, saiga populations have declined by more than 90% because of overhunting (Milner-Gulland *et al.*, 2003). As a result of lack of ecological knowledge about saiga migrations and since much has changed in the saiga range in terms of population numbers, favourable habitat and land use, there is an urgent need to assess the factors driving saiga migrations to different seasonal ranges and habitat selection within the seasonal ranges. It is also important to identify whether there have been changes in the species' migratory habitat selection in response to the enormous changes to the context within which migration takes place.

This study is designed to provide a quantitative baseline for research on saiga migration. We first focus on the differences and similarities between the four remaining migratory saiga populations, which occur over vast areas that differ in climatic conditions, resource availability and geography. We predict at the entire saiga range scale, the 'between-population seasonal ranges' of each of the four populations differ from each other, but broadly all populations migrate in a similar manner from south to north (H_1). Second, we address whether differences in productivity or precipitation drive migration of each of the four populations. If precipitation drives migration, saigas will select areas with relatively higher average precipitation in the growing season (spring and summer) and avoid these areas in winter, and this trend will be consistent for all the populations (H_2). If migration is driven by resource abundance, saigas will select areas with relatively higher productivity in all seasons (the current seasonal range will have higher productivity than the previous seasonal range), and this trend will be consistent for all the populations (H_3). Habitat selection within seasonal ranges could depend on either the predictability or average level of productivity of an area or on the productivity of that area during a specific year. We predict that selection within seasonal ranges is on the basis of peak productivity in a particular year, since the region is characterized by large interannual variations in productivity (H_4). We also predict that saiga migration has been robust to recent changes in population size, density and habitat and hence that the drivers of migration in recent years are similar to those for the period as a whole (H_5). Finally, we discuss the key threats to migration and propose conservation actions for saiga populations.

METHODS

Study area

The Republic of Kazakhstan is generally flat in the saiga range, covered by treeless steppe, semi-desert and desert vegetation except in the farthest north and south. It is characterized by hot summers (30–55 °C) and severe winters (–20 to –45 °C). Vegetation zones occur in a latitudinal gradient. The northernmost steppe zone with an annual precipitation above 300 mm is dominated by grasses such as *Stipa lessinga*, *S. capillata*, *S. sareptana*, *Festuca valesica*, *Poa* and *Agropyron*

species. The semi-desert zone just below the northern steppe typically has a precipitation of 200–250 mm per year and contains associations of *Stipa* and *Festuca* species as well as areas dominated by *Artemesia* species. Precipitation in the southerly desert zone is <200 mm annually. This zone is dominated by plant species such as *Artemesia terrae-albae* and *Artemesia turanica* in its northerly areas, and by saltworts and other xerophytic species (e.g. *Salsola*, *Anabasis*, *Atriplex cana*, *Halochnemum*, *Kalidium* and *Phragmites australis*) to the south and east. The saiga population in the pre-Caspian region of Russia is now restricted to the Republic of Kalmykia and Astrakhan province (Fig. 1) situated in the steppe and semi-desert region. This area is dominated by species such as *Stipa* and *Festuca* spp. and some small shrubs such as *Artemesia* and *Salsola* spp., and precipitation increases from the semi-desert in the southeast (170–200 mm) to the steppe in the northwest (350–400 mm; Kühl, 2008).

To identify the historical seasonal ranges and migratory habitat used by saigas, we collated information from books, published articles and other Russian language sources (e.g. Bannikov *et al.*, 1961; Fadeev & Sludskii, 1982; Grachev &

Bekenov, 1993; Bekenov *et al.*, 1998). We did not consider the Mongolian subspecies as it differs from the nominate subspecies both biologically and in its habitat use and is less clearly migratory (Berger *et al.*, 2008). Currently, 75% of the saiga population occurs in three populations in Kazakhstan and 25% in one population in the pre-Caspian region of Russia, compared to their widespread distribution all over Eurasia in the past (Bekenov *et al.*, 1998; CMS, 2006). Two of the Kazakhstan-based populations of *S.t.tatarica* are trans-boundary; an unknown proportion of the Ustiurt population migrates to Uzbekistan in winter, and a small proportion of the Ural population enters Russia. The Kazakhstan populations inhabit all three vegetation zones depending on the season (Fadeev & Sludskii, 1982; Bekenov *et al.*, 1998), whereas the pre-Caspian population generally inhabits the semi-desert, travelling north to the steppe only when there is heavy snow or drought (Lushchekina & Struchkov, 2001). 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. The period, route, distance and speed of migration differ from year to year and among the

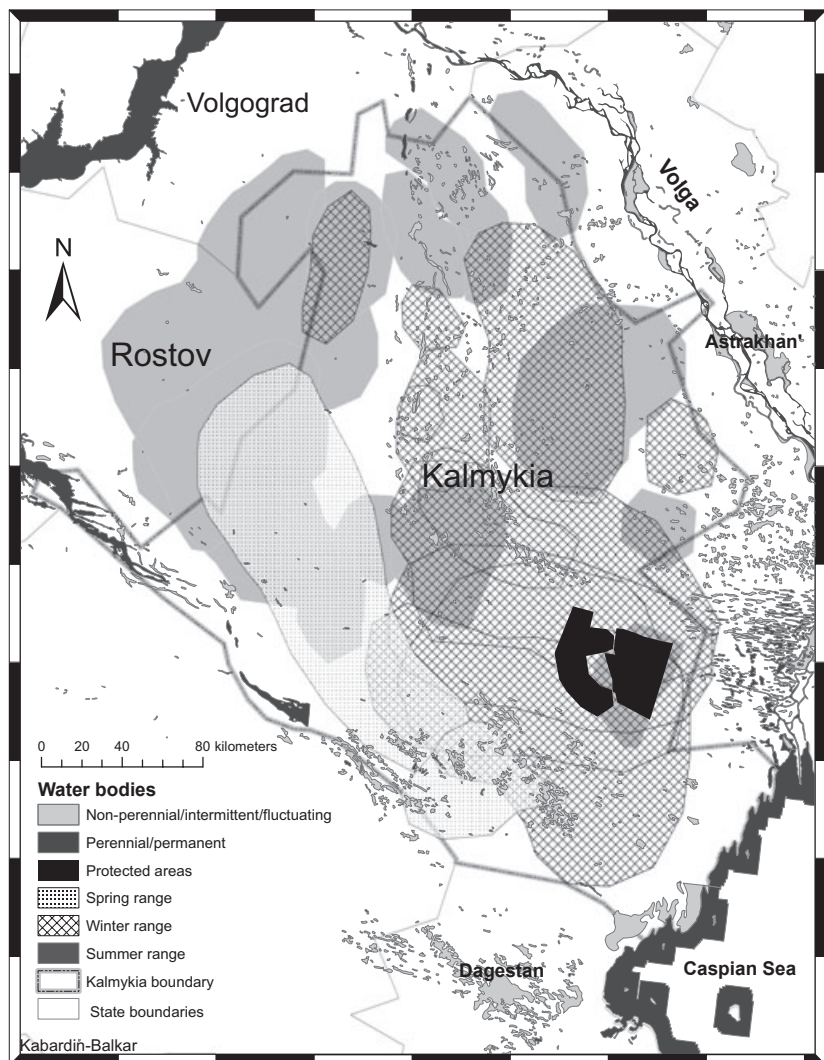


Figure 1 Historical ranges of the pre-Caspian saiga antelope population during spring (early/mid-March to early June), summer (early/mid-June to early/mid-September) and winter (November to early/mid-March) in the Republic of Kalmykia and the surrounding provinces (adapted from Bannikov *et al.*, 1961 and Lushchekina & Struchkov, 2001).

three different Kazakhstan-based populations, but are only qualitatively known. Roughly, the Betpak-Dala population may cover 600–1200 km each way, the Ustiurt population 300–600 km, and the Ural population 200–300 km during migration (Bekenov *et al.*, 1998). There is no information on the proportion of animals migrating every year or on the timing of migration.

Data sources

The Institute of Zoology of Kazakhstan carries out annual aerial surveys over most of the saiga's range in Kazakhstan, during the spring migration period (March–May). Saiga group concentrations and aerial transects are recorded as polygons on topographical maps during the surveys. Ground vehicular surveys are also conducted in areas which are not covered during the aerial surveys or which are more accessible on the ground at other times of the year. Observations of saigas during the ground surveys are recorded as point locations. We used survey reports covering the time period 1970–2008 to identify where saigas concentrate during the summer (ground survey), spring (aerial survey) and winter (ground survey) periods. These data have been recorded consistently and provide a valuable source of insight into the saiga's long-distance migrations during this period. We transferred the observations into point locations in a geographical information system (GIS). As the observations were irregular in time, all the available locations were initially pooled to identify the general migratory range in Kazakhstan. In the pre-Caspian population, formal population surveys were not carried out, so we referred to the historical saiga ranges identified by Bannikov *et al.* (1961) and Lushchekina & Struchkov (2001). No robust data were available for Uzbekistan or Turkmenistan or from the Russian part of the Ural population.

The number of sites recorded for each Kazakhstan population in different seasons were as follows: Betpak-Dala summer 221, spring 126 and winter 265, Ural summer 36, spring 36, winter 29, Ustiurt summer 34, spring 47, winter 21. We created minimum convex polygons based on all observations for each season over the total study period to delineate the extent of each seasonal range within which to sample random points. The historical data for the pre-Caspian population were already presented in the form of polygons (Fig. 1). We sampled 400 random points in each of the seasonal polygons of the Kazakhstan populations to estimate the seasonal characteristics of the ranges in terms of the studied variables, and 800 for the pre-Caspian population as a result of its larger range area. The number of points sampled was chosen to obtain a representative sample of the entire range. There is no established rule to decide the minimum sample sizes for random points (Peng *et al.*, 2002). In the absence of a general rule, it is usually assumed that the greater the sample size, the more accurate the model (Cumming, 2000). Small sample sizes reduce a model's predictive power, but after a certain threshold, the model predictions become independent of sample size (Jiménez-Valverde *et al.*, 2009).

Variables

The topographical, vegetation and bioclimatic variables were extracted from raster maps obtained from a range of sources. A digital elevational model (90-m resolution) was acquired from Surface Radar Topography Mission (SRTM) data (<http://www2.jpl.nasa.gov/srtm/>). Altitude (m) and slope (°) were extracted from the DEM for the entire saiga range using the 'Spatial Analyst' extension in the ArcGIS 9.2. Monthly and annual averages in precipitation (mm) were acquired from the WorldClim database (Hijmans *et al.*, 2005, 2006, <http://www.worldclim.org/>), in the form of raster grids. These fine resolution (~1 km) spatial data were interpolated from weather stations across the globe, with averages calculated from at least 10 years of data (Hijmans *et al.*, 2005, 2006). The variables were derived from mean monthly and quarterly climate estimates to approximate energy and water balances at a given location (<http://www.worldclim.org/bioclim.htm>). To identify the average vegetation productivity of the seasonal range, annual range and transition areas, we acquired at 1-km resolution, 16-day normalized difference vegetation index (NDVI) scenes, for the period 2000–2008, from moderate resolution imaging spectro-radiometer (MODIS) instruments aboard NASA's Terra satellite (Global Land Cover Facility, <https://wist.echo.nasa.gov/wist-bin/api/ims.cgi?mode=MAINSRCH&JS=1>). We did not use recently available NDVI data for the period 1981–2006 at the 8 × 8 km scale in order that the NDVI and precipitation analyses were undertaken on the same scale and to the same end date. Models using 1 × 1 km MODIS and 8 × 8 km GIMMS datasets gave similar results (see Table S1). NDVI is used as an index of vegetation greenness and above ground primary productivity (Ito *et al.*, 2005, 2006; Pettorelli *et al.*, 2005). It works well as an index of vegetation productivity and quality even for grasslands because healthy green vegetation reflects strongly in the near-infrared but absorbs most light in the red band (Paruelo *et al.*, 1997; Kawamura *et al.*, 2003). In addition to the topographical, vegetation and climatic variables, we also recorded the geographical coordinates for each saiga group sighting and projected then into Universal Transverse Mercator (UTM) projection (Zones 38–43 N). The values for these variables for the saiga points were extracted using the Point Intersect tool, in the Hawth's Tools extension of ArcGIS 9.2 (ESRI Inc., Redlands, CA, USA).

DATA ANALYSES

Seasonal trends of NDVI and Precipitation

Seasons were defined with reference to Bekenov *et al.*, 1998 based on precipitation timing and temperature changes; spring (early/mid-March to early June), summer (early/mid-June to early/mid-September), autumn (mid/late September to early November) and winter (November to early/mid-March). For testing H_1 , H_2 and H_3 , we used the full dataset of historical observations from Kazakhstan and the pre-Caspian. To assess the pattern of changing climatic and resource conditions in the

area, we monitored changes in mean monthly NDVI and precipitation over the year by extracting the values from the respective rasters. Mean NDVI in the range area overall was subtracted from each of the values for the summer and winter ranges for every month to obtain an index of relative NDVI in the different seasonal ranges within the full range (Leimgruber *et al.*, 2001; Ito *et al.*, 2006).

General population and range characteristics across seasons

The general characteristics of each population's seasonal ranges were assessed by comparing the average values of altitude, slope, latitude, NDVI and precipitation for the locations used by saigas in the spring, summer and winter seasons (H_1). We performed a discriminant analyses (DA) to identify the differences between the seasonal ranges and among populations. Four populations and three seasons were included as response variables and altitude, slope, NDVI, precipitation and latitude as explanatory variables. The variables were assessed for their concordance with the assumptions of DA, of multivariate normality and equality of the variance–covariance structure (Ripley, 1996; Venables & Ripley, 2002).

Drivers of migration

To identify the drivers of migration (H_2 and H_3), we analysed each of the populations separately. As changes in forage quality and precipitation have been regarded as among the main drivers of ungulate migration (Bolger *et al.*, 2008; Harris *et al.*, 2009), we used these variables in a use availability framework to identify the differences between the used and random sites in different seasons. The value of NDVI for each season was estimated as the average of the NDVI of all the months included in the period. We took an average NDVI rather than integrated NDVI (Pettorelli *et al.*, 2005; Hamel *et al.*, 2009), as we were testing differences among the seasonal ranges based on NDVI values from unmarked saiga locations. INdVI would be an appropriate measure for testing for the timing of green up or of the onset of migration related to saiga locations. The value for total precipitation for each season was the sum of average precipitation for all the months within the season.

Binomial logistic regression models with a logit link were used to identify the appropriate combination of variables separating the used from the random sites (Venables & Ripley, 2002). All the predictor variables were assessed for normality and appropriately transformed when required. Model simplification was performed through stepwise deletion using likelihood ratio tests (LRT), which are based on differences in the deviances. Non-linear relationships in the models were assessed using partial residuals and were adequately addressed by including the second order polynomial for each of the variables showing non-linearity. Models containing quadratic terms without the linear terms were discarded. To assess the goodness of fit of models, we used the Pearson's chi-square statistic (Hope, 1968).

NDVI, precipitation, latitude of each site and interactions between them were chosen as predictor variables with season as a three-level factor. Altitude and slope were not used, as these had not emerged as relevant in the DA and varied little over the saiga range. We included latitude because of a strong latitudinal gradient in vegetation type in the study area which probably interacts with NDVI and precipitation. NDVI and precipitation were not found to be correlated ($r = 0.05$, 95% CI: -0.0028 , 0.10) or collinear (VIF = 1.002). Robinson (2000), however, analysed the relationships between precipitation and NDVI in the saiga range in Kazakhstan and found that precipitation was a reasonable predictor of peak annual NDVI, although much of the variance in the relationship was because of site effects. The author also suggested that the relevant precipitation period influencing biomass varied from site to site, and monthly or annual precipitation may therefore not be a good predictor of above ground biomass. It is the precipitation in an entire period which may influence the peak NDVI during a year, along with an additional annual precipitation effect. She identified year as the single best predictor of NDVI at all sites, and precipitation in winter and spring had the greatest effect on NDVI and especially on peak NDVI. Hence, we analysed precipitation and NDVI separately to identify their importance independently of each other and because of these difficulties in separating their effects in previous studies.

Habitat selection within the seasonal range

To test for habitat selection within seasonal ranges and changes in migration pattern (H_4 and H_5), we adopted a similar analysis as for assessing the drivers of saiga migration but using observations from the last decade (2000–2008) and the corresponding NDVI. Consistent precipitation data were not available for the entire period; hence, only NDVI was used to test these hypotheses. Only data from Kazakhstan were considered, as the data collection in the pre-Caspian region within the time period considered was restricted to protected areas in the saigas' winter range (Fig. 1). Only summer and winter ranges were considered for the analysis, because habitat selection only takes place within these seasons, as the animals are on the move during spring and autumn. The random sites were separately sampled from within each of the seasonal ranges. The number of used and random sites for each population was as follows: Betpak-Dala: Summer Used 46, Winter Used 56, Random 493. Ustiurt: Summer Used 26, Winter Used 32, Random 196. Ural: Summer Used 23, Winter Used 30, Random 272. For the winter sites in the Ustiurt population, we only used sightings from Kazakhstan, as they were consistently available throughout the considered period. Hence, no conclusion can be drawn about the winter range in Uzbekistan and Turkmenistan.

We tested for spatial autocorrelation among all the pooled saiga locations within each range and within each season using Moran's Index (Cliff & Ord, 1981). Moran's I is used to estimate the strength of the correlation between observations as a function of the distance separating them (correlograms).

The values of Moran's *I* range from +1 meaning strong positive spatial autocorrelation to 0 meaning a random pattern to -1 indicating strong negative spatial autocorrelation. We did not do a global test for autocorrelation for the pooled data as the data covered a large spatial scale and a diverse range of habitat types. The Moran index was positive but not significant in all cases (Betpak-Dala: Summer 0.278, Winter 0.256, Ustiurt: Summer 0.351, Winter 0.325, Ural: Summer 0.287, Winter 0.212); hence, no autocorrelation terms were considered in the models.

Values for NDVI in the year of observation, average NDVI of the site during 2000–2008, the logged coefficient of variation of NDVI for the site, season (summer and winter) and year (2000–2008) were included in a binomial logistic regression framework, using the same modelling procedures as outlined above. Since all NDVI variables showed non-linearity for all three populations as assessed by the partial residuals, second-order polynomials were used for annual and average NDVI, and the CV was log-transformed. All the statistical analysis was carried out in R 2.7.2 (R Development Core Team, 2008).

RESULTS

Seasonal trends in NDVI and Precipitation

We compared the summer, spring and winter seasonal ranges of saigas to identify differences between them. Monthly averages for NDVI show strong seasonal patterns in resource availability, where the highest average values occur in April–June (mean \pm S.E: 0.43 ± 0.13) and the lowest average values in January–February (0.02 ± 0.01 ; Fig. 2a). The peak values, however, vary from year to year. Differences in average NDVI values between the three seasonal ranges are most pronounced in the maximum values in spring and summer and the minimum values in winter. Relative differences in NDVI (Fig. 2b) suggest a strong difference between the summer and winter ranges, with a rapid switch in NDVI during spring. The spring ranges maintain a reasonably high NDVI throughout the year except in winter. The winter ranges have the relatively lowest NDVI during the summer season and relatively highest values in winter.

The monthly trends in precipitation (Fig. 2c) show high precipitation in the summer ranges in the summer season with a peak in July, whereas the winter ranges receive much lower precipitation in summer, with the lowest levels in August–September. The summer ranges also continue to receive higher precipitation in winter compared to the winter ranges. The spring precipitation trend appears to be intermediate between the summer and winter ranges, although the peaks in precipitation in the spring ranges occurred during early spring (March–April) and late autumn (October–November).

General range characteristics across seasons

As a descriptive tool DA showed clear differences in NDVI, precipitation and latitude between the saiga's seasonal ranges

for all four populations (H_1). The analysis identified two main discriminant axes (eigenvalues: 0.95 and 0.87, Table 1) on which the categorical variables for population and season were separated. The first axis was mainly associated with latitude (Fig. 3a, score 1.09) and the second axis with precipitation (-0.97) and NDVI (0.36). On the basis of individual class scores, all four populations showed clear separation between the seasonal ranges and strong association with latitude indicated by the decreasing score of latitude from winter to summer ranges (Table 1, Fig. 3b; as the coordinates were in UTM, lower values of scores indicate higher latitudes). For example in the case of Betpak-Dala, the latitude variable scores for winter, spring and summer ranges were 1.65, 1.31 and 1.17 respectively. With reference to the second axis, all populations showed positive association of spring ranges with NDVI and had the highest scores for the spring season (Table 1, Fig. 3a). Most of populations showed a positive association with precipitation for the summer ranges, except Ustiurt (Fig. 3b). The summer range of the pre-Caspian population occurred in the areas with highest summer precipitation followed by Ural, Betpak-Dala and Ustiurt. The slope variable did not contribute significantly in separating the habitat characteristics of different populations, indicating that overall all the populations used areas of similar topography.

Drivers of migration

NDVI, precipitation, season and latitude emerged as significant predictors in the logistic regression models (consistent with the predictions of H_2 & H_3). However, NDVI, precipitation and latitude always occurred with their second-order polynomials (Table 2 Set A & B), indicating the selection of intermediate values of these variables by saigas. This trend was consistent for all populations. However, there were differences in the interactions among these variables. NDVI interacted negatively with latitude in the pre-Caspian (-0.56 ± 0.08) and Betpak-Dala (-0.22 ± 0.12) populations (Table 2 Set A), whereas the precipitation–latitude interaction was positive for Betpak-Dala (0.34 ± 0.11) and negative for the Ural (-4.23 ± 1.59) and pre-Caspian (-1.59 ± 0.41) populations (Table 2 Set B). The NDVI–season interaction was positive for all populations except Ustiurt with summer ranges having higher NDVI (Table 2 Set A). For all populations, summer ranges had higher precipitation than winter ranges indicated by higher estimates (Table 2 Set B). The relationship of seasonal range and latitude was similar in most cases; summer ranges were always at higher latitude, and winter ranges at lower latitude compared to spring ranges.

Interannual variation in habitat selection within the seasonal range

Within the seasonal ranges, only the Ural population selected habitat with intermediate current-year NDVI (estimates - NDVI_y: 59.14, NDVI_{y2}: -64.30, Table 3); the other three

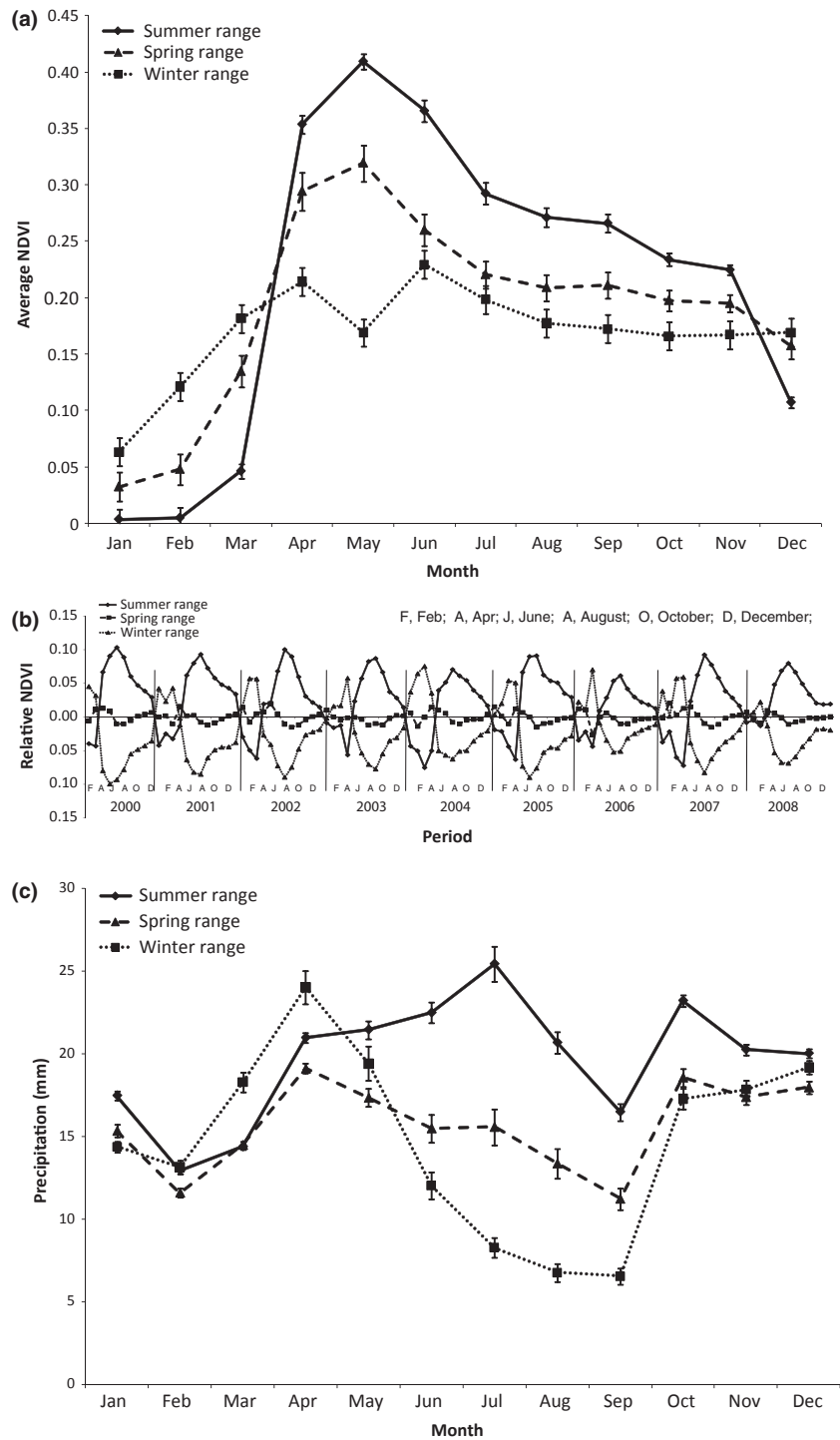


Figure 2 (a) Annual pattern of primary productivity in the saiga antelope range in Kazakhstan and the pre-Caspian region, measured as average normalized difference vegetation index (NDVI) per month for the summer (early/mid-June to early/mid-September), winter (November to early/mid-March) and spring (early/mid-March to early June) ranges. Error bars represent the 95% confidence intervals. (b) Seasonal changes in relative normalized difference vegetation index (NDVI) in the summer, spring and winter ranges of the saiga antelope in Kazakhstan. Positive and negative values mean higher and lower NDVI values than the average in the annual ranges, respectively. (c) Average monthly precipitation pattern (in mm) in the saiga antelope's summer, spring and winter ranges in Kazakhstan.

populations consistently selected habitat on the basis of intermediate average NDVI (NDVI_a, NDVI_{a2}: Betpak-Dala 55.87, -105.04, Ustiurt: 42.095, -88.48, Table 3), contrary to H4. Also, the Betpak-Dala and Ural populations selected habitat with low interannual variability in NDVI. Season negatively interacted with average NDVI and variability of NDVI for Betpak-Dala and with current-year NDVI and variability of NDVI for Ustiurt (Table 3). Hence, at the within-

season range selection scale, an intermediate range of average NDVI and lower variability were generally the significant variables distinguishing the used from random sites. As predicted by H5, NDVI was a driver of habitat use in the summer and winter ranges for all three Kazakhstan populations during the last decade, as it was for the dataset as a whole, although the significance of NDVI-derived variables varied between populations.

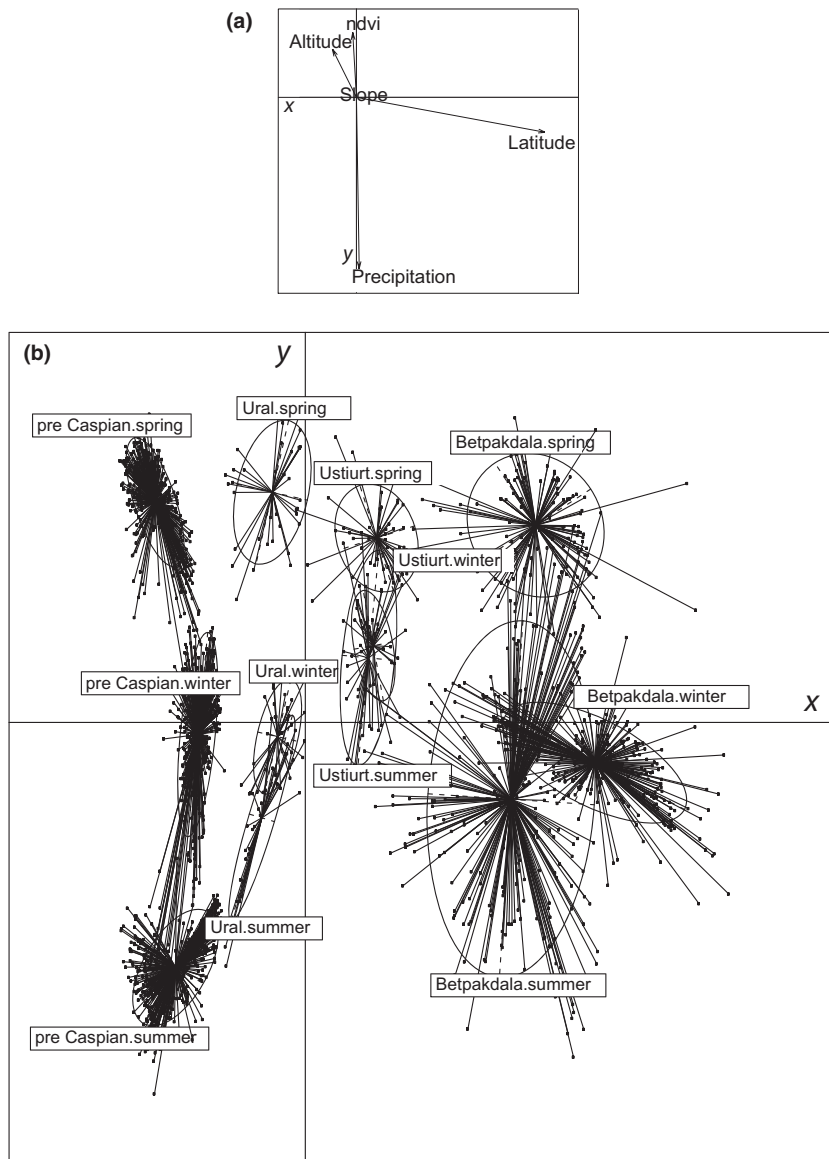


Figure 3 (a) Discriminant analysis of *Saiga tatarica* populations and their seasonal ranges in Kazakhstan and the pre-Caspian. Population and season are categorical variables and altitude (m), latitude, slope ($^{\circ}$), normalised difference vegetation index (NDVI) and seasonal precipitation (mm) are explanatory variables. The canonical weights for each distinguishing variable are given with respect to the axes. 'x' represents the first discriminant axis and 'y' the second axis. (b) Scores of the functions 'populations (pre-Caspian, Ural, Ustiurt, Betpak-Dala)' and 'seasons (summer, spring, winter)' from the discriminant analyses, plotted together for each saiga antelope population of Kazakhstan and the pre-Caspian region, with each individual/group location. Each line with a dot at the end arising from the centre of each ellipse represents one saiga location. The first factor axis (eigenvalue: 0.958) is represented by latitude, and the second axis (0.877) is represented by NDVI and precipitation (also see Fig. 4a).

DISCUSSION

The four saiga populations differ in the characteristics of their broad seasonal ranges, being spread over a vast landscape with local and broad-scale topographical and climatic conditions varying with latitude and longitude (H_1). All four populations undertake migrations following a latitudinal gradient in vegetation productivity determined by precipitation, with summer ranges at highest latitudes followed by spring ranges and then winter ranges at the lowest latitudes. The presence of such a gradient explains why the saiga migration in Kazakhstan always follows a north–south direction (Bekenov *et al.*, 1998). The Ustiurt population shows a relatively weaker association with precipitation, which is probably because of its confinement to the desert and semi-desert areas, which receive relatively less precipitation than the steppe at higher latitudes. It is not clear why this population does not utilize steppe areas. Possible reasons for future investigation could be habitat

modifications during the Soviet virgin lands campaign which may have rendered steppe areas unfavourable, or the presence of barriers and disturbance in these areas (McCauley, 1976; Medvedev, 1987). The pre-Caspian population shows high association with precipitation and shows a much less clear north–south migratory pattern than the other three. This is probably because of the generally higher precipitation in the area closer to Caspian, leading to the lack of a desert zone in the area and hence the population's occurrence in semi-desert and steppe areas all year round (Fig. 1). Hence, NDVI, precipitation, latitude and their interactions clearly explain the observed migration patterns for all populations at the studied scale. The significant interactions of both NDVI and precipitation with latitude demonstrate that these variables are closely coupled, but not directly correlated.

We observed a rapid shift in NDVI during the onset of spring (March–May), which may be the cue initiating migration to higher latitudes (H_2). The selection of intermediate

Table 1 Class scores for each combination of the four populations of Saiga antelope (*Saiga tatarica*) in Kazakhstan and the pre-Caspian and the three seasons on the two dominant axes of the discriminant analyses

	Discriminant axis 1	Discriminant axis 2
Betpak-Dala. spring	1.3151	1.1264
Pre-Caspian. spring	-0.8579	1.2575
Ural. spring	-0.1884	1.3147
Ustiurt. spring	0.4072	1.0531
Betpak-Dala. summer	1.1753	-0.4388
Pre-Caspian. summer	-0.7414	-1.3994
Ural. summer	-0.2481	-0.5449
Ustiurt. summer	0.3607	0.3686
Betpak-Dala. winter	1.6536	-0.2298
Pre-Caspian. winter	-0.6143	-0.0694
Ural. winter	-0.1585	-0.0813
Ustiurt. winter	0.3882	0.4384

values for NDVI in spring at the broad scale is likely to be a by-product of saigas passing through these areas on the way to their summer range. However, the same pattern is observed at the within-season scale, suggesting a probable quality–quantity trade-off in the vegetation being selected. This preference for areas of intermediate NDVI echoes the pattern also found for the Mongolian gazelle (*Procapra guttorosa*), a comparable species in terms of body size and ecology. Mueller *et al.* (2008) suggest that the trade-off may relate to low NDVI (as an index of biomass) limiting ingestion rates and areas with high NDVI having mature forage with low digestibility.

The fact that in the period 2000–2008, saigas appear to be selecting habitat within the seasonal range based on intermediate average NDVI and low variability rather than current-year NDVI values suggests that the species' needs are consistent between the broader and the finer spatial scales, irrespective of the high variability in NDVI between years (H_4). This consistency also suggests that despite a massive reduction in population sizes and an accompanying severe reduction in

Table 2 Results of binomial logistic regression models (standardized estimates) including the normalized difference vegetation index (NDVI; set A) and precipitation (PREC; set B) for identifying the drivers of saiga antelope migration in Kazakhstan and the pre-Caspian region of Russia

	Betpak-Dala			Ustiurt			Ural			Pre-Caspian		
	Estimate	SE	P Value	Estimate	SE	P Value	Estimate	SE	P Value	Estimate	SE	P Value
Set A – NDVI												
Intercept	-1.471	0.172	<0.001	-13.274	1.875	<0.001	-2.003	0.288	<0.001	-0.565	0.120	<0.001
NDVI	1.650	0.238	<0.001	4.616	0.683	<0.001	2.029	0.596	<0.001	0.357	0.130	<0.001
NDVI ²	-1.100	0.120	<0.001	-1.319	0.211	<0.001	-1.451	0.386	<0.001	-0.167	0.060	<0.01
Latitude	0.541	0.159	<0.001	1.308	5.468	<0.001	-1.350	0.334	<0.01	-1.239	0.124	<0.001
Latitude ²	-0.346	0.064	<0.001	-1.408	0.245	<0.001	-0.985	0.217	<0.001	-0.485	0.055	<0.001
Factor (season) summer	0.190	0.218	<1	0.169	1.164	<1	0.575	0.467	<0.05	0.165	0.153	<0.05
Factor (season) winter	2.558	0.220	<1	2.667	1.275	<0.05	0.652	0.565	<0.1	0.215	0.147	<0.001
NDVI: summer	0.552	0.221	<0.05				-1.848	0.726	<0.05	0.483	0.191	<0.05
NDVI: winter	-0.470	0.410	<1				-1.881	1.184	<1	0.630	0.201	<0.01
Latitude: summer	-0.326	0.182	<0.1	-0.217	0.430	<1	-1.096	0.458	<0.05	0.622	0.168	<0.001
Latitude: winter	0.672	0.226	<0.01	-1.236	0.513	<0.05	0.073	0.424	<1	1.806	0.169	<0.001
NDVI × Latitude	-0.221	0.122	<0.1							-0.565	0.085	<0.001
Residual deviance	2120.1			552.9			603.56			4098.9		
Degree of freedom	2402			1295			1293			3588		
Set B – PREC												
Intercept	-2.178	0.334	<0.001	-9.404	1.715	<0.001	-14.571	3.284	<1	-0.949	1.053	<0.001
PREC	-1.488	0.425	<1	1.690	0.935	<0.05	-16.259	4.056	<0.1	-1.685	1.267	<1
PREC ²	-0.415	0.066	<0.001	-0.858	0.265	<0.01	-4.852	1.438	<0.001	-1.478	0.443	<0.001
Latitude	0.065	0.178	<0.001	5.903	1.273	<0.001	-6.886	2.039	<0.05	-2.876	0.509	<0.001
Latitude ²	-0.400	0.063	<0.001	-1.178	0.232	<0.001	-1.376	0.464	<0.01	-0.712	0.116	<0.001
Factor (season) summer	-0.952	0.367	<1	-5.418	1.654	<0.001	12.042	3.319	<0.001	0.286	1.014	<0.01
Factor (season) winter	-1.655	0.644	<0.001	3.107	1.819	<1	11.879	3.232	<0.05	0.470	1.091	<0.001
PREC: summer	2.995	0.486	<0.001	2.935	0.7889	<0.001	19.170	4.856	<0.001	3.547	2.175	<1
PREC: winter	1.746	0.480	<0.001	-0.060	0.955	<1	10.112	3.342	<0.01	1.502	1.346	<1
Latitude: summer	-1.235	0.291	<0.001	0.243	0.438	<1	6.524	2.429	<0.01	3.449	0.957	<0.001
Latitude: winter	0.335	0.209	<1	-1.227	0.542	<0.05	3.914	1.591	<0.05	3.458	0.516	<0.001
PREC × Latitude	0.348	0.110	<0.01				-4.236	1.591	<0.01	-1.599	0.417	<0.001
Residual deviance	2364.4			571.11			569.6			4130.8		
Degree of freedom	2402			1293			1292			3588		

The terms followed by ² denote second-order polynomials. Spring is the baseline for the factor season. The unit for latitude is metres (UTM).

Table 3 Results of binomial logistic regression models for habitat selection within the seasonal range for saiga antelope locations in 2000–2008 from the four Kazakhstan populations

Population/Season	Current NDVI (NDVI _y)	NDVI _y ²	Average NDVI (NDVI _a)	NDVI _a ²	CV of NDVI
Betpak-Dala summer	0	0	–	++	---
Betpak-Dala winter	0		+		++
Betpak-Dala winter *NDVI			–		+
Ustiurt summer	0	0	+	+	0
Ustiurt winter	--		++		–
Ustiurt winter *NDVI	+++				--
Ural summer	+++	---	+	0	---
Ural winter	+++		0		+

Significant codes: +++ Positive Estimates <0.001, --- Negative Estimates <0.001, ++/--<0.01, +/- <0.05, 0 Not Significant. Suffix ²: Second-order polynomial, *NDVI: Interaction term between the population (season) and the normalized difference vegetation index (NDVI)-related variable.

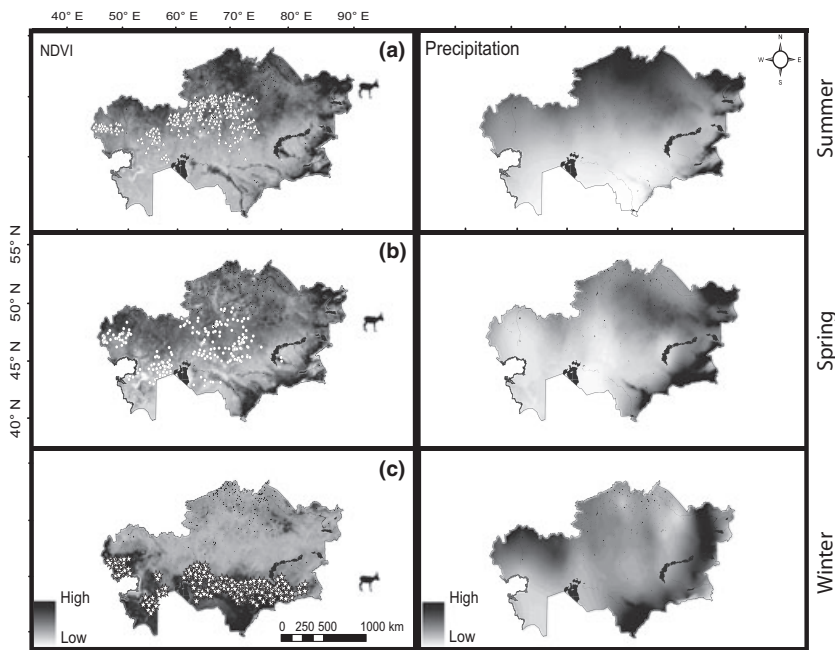


Figure 4 Latitudinal gradient observed in the productivity (standardized normalized difference vegetation index, NDVI) and precipitation across Kazakhstan and saiga antelope group locations by season. The symbols represent the (a) summer, (b) spring and (c) winter locations. Major water bodies are represented in black.

herd sizes and densities since the mid-1990s (Kühl, 2008; McConville *et al.*, 2009), as well as disruption to reproductive behaviour (Milner-Gulland *et al.*, 2001; Kühl *et al.*, 2007), saiga migrations are still intact (H₅). Nevertheless, our results concerning fine-scale habitat selection need to be treated with caution, because they are only available for this period of population disruption. The data on habitat selection are also potentially biased due to poor detectability of small herds (McConville *et al.*, 2009). Hunting has substantially increased the saiga’s wariness of humans in the last decade, potentially changing their use of habitat in areas near human settlement and also reducing detectability (IUG/EJMG, pers. obs.; Singh *et al.*, 2010). Conversely, the exodus of livestock from many areas of the saiga’s range and the subsequent improvement in pasture quality (de Beurs & Henebry, 2004; Kerven *et al.*, 2006) may have reduced the negative impacts of direct and indirect competition for grazing, particularly in the winter range,

potentially substantially reducing the constraints on habitat selection experienced in previous years (Robinson & Milner-Gulland, 2003). Future surveys, with sampling bias accounted for, could elucidate the effect of these various constraints on habitat selection at the fine scale.

Conservation and threats

The migratory nature of saigas makes establishment of protected areas a challenging task. Currently, few protected areas dedicated to saigas exist in Kazakhstan (but see Klebelsberg, 2008). The pre-Caspian population has received recent protection through establishment of the Chernye Zemli Biosphere Reserve and Stepnoi Reserve along with increased ranger monitoring (Kühl, 2008). However, it is still not clear what proportion of the population remains in unprotected areas at different times of the year (Leon, 2009). A focus on

specific small protected areas risks curtailing the annual seasonal migrations because of herds remaining in the relatively undisturbed locations within their winter range rather than risking venturing out into the more heavily populated areas. Additional information on saiga distribution outside these areas is therefore required to assess the status of saiga populations and their migrations in the pre-Caspian region. On a much larger scale, it is still completely unclear what proportion of the Ustiurt population migrates to Uzbekistan during the winter, and how this proportion varies between years. Similarly, the importance of Uzbekistan as a spring or summer range is not clear, although it is known that small groups of animals do give birth there (Bykova *et al.*, 2008). Urgent cooperation between the Kazakhstan and Uzbekistan saiga management authorities is required to resolve these uncertainties and institute appropriate protection for this population year-round. Even less is known about the movements and status of the Ural population (CMS, 2006).

Climate change models from the Intergovernmental Panel on Climate Change (IPCC) predict that winter precipitation is likely to increase and summer precipitation to decrease in Central Asia, with most models predicting net annual increases in the north and east of the region and net annual decreases in the south and west (IPCC, 2007). Higher winter precipitation means higher snow in winter, which is a limiting factor for the saiga population that we have demonstrated to be an important driver of migrations. Lower summer precipitation means lower NDVI eventually in the summer areas and hence lower forage availability during the crucial spring and summer seasons. Elucidating the impacts that these changes will have on saiga migrations and on their life history, and how they will interact with other human-induced habitat modifications remain a future challenge.

Considering these threats to saiga migrations and gaps in knowledge, it is important that detailed studies are carried out on saiga ecology and behaviour during migration. Long-distance migrations are on the decline globally due to many of the same factors observed for saigas. A majority of these factors are common throughout, such as socio-political changes, habitat conversion to agriculture or urbanization, lack of protected areas and poaching (Bolger *et al.*, 2008; Harris *et al.*, 2009). This suggests that it would be productive for organizations such as the Convention on Migratory Species, which are working to conserve migration as a behaviour, to establish strategies to counter common problems as well as designing species-specific conservation and recovery programmes. Studies at finer scales, focusing on patch selection during migration, and the effects of distance to water sources and man-made barriers, may provide deeper insights into the factors affecting broader-scale saiga movement patterns during migration.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Model results for 1×1 km MODIS and 8×8 km GIMMS datasets for selection of habitat within the seasonal ranges by the saiga antelope.

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BIOSKETCH

Navinder J. Singh is a Post Doctoral Research Associate studying conservation ecology of the saiga antelope in rangelands and deserts of Central Asia. The major work focus of the research group is on 'Optimizing monitoring as a conservation tool'. <http://www.iccs.org.uk/research-monitoring.htm>.

Author contributions: N.J.S. and E.J.M.G. conceived the ideas, designed the study, analysed the data and wrote the Manuscript. I.G. and A.B. collected the saiga data; N.J.S. prepared and organized the satellite data.

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