



Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Spatiotemporal habitat dynamics of ungulates in unpredictable environments: The khulan (*Equus hemionus*) in the Mongolian Gobi desert as a case study

Dejid Nandintsetseg^{a,b,*}, Petra Kaczensky^c, Oyunsai Khan Ganbaatar^{d,e}, Peter Leimgruber^f, Thomas Mueller^{a,b,f}^a Senckenberg Biodiversity and Climate Research Centre, Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, Frankfurt (Main), Germany^b Department of Biological Sciences, Goethe University Frankfurt, Max-von-Laue-Straße 9, 60438 Frankfurt (Main), Germany^c Research Institute of Wildlife Ecology, University of Veterinary Medicine, Vienna, Savoyenstrasse 1, Vienna, Austria^d Great Gobi B Strictly Protected Area Administration, Mongolia^e International Takhi Group, Baigali Ordon, Ulaanbaatar, Mongolia^f Smithsonian Conservation Biology Institute, National Zoological Park, Front Royal, VA, USA

ARTICLE INFO

Article history:

Received 13 April 2016

Received in revised form 11 October 2016

Accepted 18 October 2016

Available online xxxxx

Keywords:

Nomadic movement

Habitat dynamic

Water availability

Dryland

Khulan

Habitat connectivity

ABSTRACT

In resource-poor environments many large herbivores do not perform seasonal migrations but show unpredictable, long-range movements within a given season. The few studies that have examined drivers for within season long-range movements suggest that these movements are a response to spatiotemporal dynamics of foraging resources.

We tested this hypothesis and were especially interested in detecting dynamics of foraging habitat which may influence high mobility of khulan, *Equus hemionus*, during summers in the Dzungarian Gobi of Mongolia. We used six years of ground census data combined with remotely sensed imagery of vegetation productivity (NDVI) to build a dynamic habitat model. We subsequently predicted khulan habitat suitability for each of the seven 16-day NDVI intervals every summer between 2004 and 2009 and examined variability of the resulting 42 prediction maps to characterize spatiotemporal dynamics in khulan foraging habitat.

Our analyses showed khulan summer foraging habitat was highly predictable with little spatiotemporal variability making it unlikely that broad scale variability of foraging habitats can explain the high mobility of khulan. The few and small areas that did show khulan habitat variability were related to locations around water sources. In addition, we found that khulan avoided habitats beyond 21 km from water sources. Together these findings suggest that water availability and switching among the sparsely located water bodies rather than broad scale dynamics of foraging habitats may be the key driver for the high mobility of khulan in the Dzungarian Gobi. Our findings highlight the importance of securing access to and connectivity among water bodies for wild ungulates and the need for further studies on possible drivers of nomadic movements in drylands.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

Long-range movements of large herbivores are often driven by dynamics of the landscape in which they forage. Especially in grass- and dry-land ecosystems many ungulates move great distances to follow foraging resources that often exhibit significant spatiotemporal variability (Fryxell et al., 2004; Fryxell and Sinclair, 1988; Mueller et al., 2011; Mueller and Fagan, 2008). When foraging resources follow predictable seasonal patterns, ungulate movements tend to be regular and seasonal, which is usually termed “migration” (Avgar et al., 2014; Dingle and

Drake, 2007). For example, in the Serengeti ecosystem, wildebeest *Connochaetes taurinus*, plains zebra *Equus quagga*, and Thomson's gazelle *Eudorcas thomsonii* migrate between the southern short grasslands in the wet season and the northern tall grasslands in the dry season (Holdo et al., 2009).

In more arid grasslands, foraging resource availability tends to be less predictable, varying not only between but also within seasons. This can be due to highly variable and patchy rainfall and snowmelt in temperate habitats (Jonzén and Knudsen, 2011). When foraging resources are temporally unpredictable, ungulates tend to move long distances even within seasons, often with little coordination among individuals. This unpredictable movement pattern has been termed “nomadism” (Mueller and Fagan, 2008; Roshier et al., 2008). One example are Mongolian gazelle *Procapra gutturosa* in Mongolia's Eastern Steppe, where long distance movements occur throughout the year irrespective of season. These long distance movements were associated

* Corresponding author at: Senckenberg Biodiversity and Climate Research Centre, Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, Frankfurt (Main), Germany.

E-mail addresses: dnandintsetseg@gmail.com, nandintsetseg.dejid@senckenberg.de (D. Nandintsetseg).

with the spatiotemporal unpredictability of foraging resources in a highly dynamic landscape (Mueller et al., 2008). Although highly mobile nomadic movements within seasons have been described in several other species or populations (Roshier et al., 2008; Singh et al., 2012; Taillon et al., 2012), the concept and its drivers remain poorly understood and little studied. In addition, nomadic species require large, unfragmented habitats. This is crucial for them to be able to move freely to respond rapidly to shifting resource availability and changing conditions over time and to cope with unpredictable resource distribution (Dean, 2004; Jonzén and Knudsen, 2011). Consequently, conserving nomadic species is a key challenge for identifying the scale of conservation management and designing conservation actions. Recent studies suggest that understanding patterns, dynamics and drivers of high mobility of animals could inform the relative importance of landscape connectivity that link important habitats or resources (Allen and Singh, 2016; Jacoby and Freeman, 2016).

The Gobi desert of Mongolia is a portion of the Central Asian Desert ecoregion often characterized by lack of surface water and predominance of low-productivity foraging resources (von Wehrden et al., 2012). It provides an important refuge for several large and wide-ranging ungulates, including the largest population of Asiatic wild ass, or khulan (*Equus hemionus*, henceforth referred to as khulan) in the world (Kaczensky et al., 2015a). While khulan are highly mobile, performing extremely long-range movements in relatively short time periods, they have no distinct migratory pattern (Kaczensky et al., 2006). In most regions of the Gobi, distribution and habitat use of ungulates are heavily affected by humans and their livestock, making it difficult to disentangle the effect of habitat use and human influence. In our study area however, the Great Gobi B Strictly Protected Area in the Dzungarian Gobi (the study area, henceforth referred to as the Dzungarian Gobi), humans and their livestock leave the protected area in summer, thus khulan spatial distribution can be expected to be primarily driven by landscape dynamics in this season. A variety of anthropogenic threats, mainly linear barriers through infrastructure projects, poaching, and competition with livestock for water sources and pasture, have resulted in khulan being listed as “Near Threatened” in the IUCN Red List (Kaczensky et al., 2015b) and if khulan mobility is linked to unpredictable resources, anthropogenic factors may impede the mobility and reduce the population viability. Hence, identifying the main drivers of their mobility is a management priority.

In this study, we determine the environmental factors predicting khulan presence during the summer vegetation period and subsequently examine the intra and inter-annual dynamics of the predicted khulan summer foraging habitat. Our habitat model and the derived prediction surfaces are built on six years of khulan occurrence data from ungulate surveys, a dynamic habitat variable based on remotely sensed imagery of vegetation productivity (Normalized Difference Vegetation Index, NDVI), and several static habitat variables (elevation, slope, distance to water and protection status). We expected that (a) vegetation productivity would be a main driver of khulan spatial distribution patterns; and (b) that khulan presence probability surfaces (subsequently also referred to as “summer foraging habitat”) would be highly variable within and among years due to high spatiotemporal variation in vegetation productivity, and thus could be a key driver for the long-range movements of khulan in the Dzungarian Gobi during summers. Our study is one of the first to examine dynamics of foraging habitat for a highly mobile species in a desert ecosystem.

2. Materials and methods

2.1. Species and study area

Khulan are one of seven wild equid species. They are predominantly grazers in summer, but also consume considerable amounts of shrubs in winter (Xu et al., 2012). As hind-gut fermenters they rely on a higher intake rate and forage abundance than ruminants in order to meet their

nutrient requirements and maximize energy (Janis, 1976). With an estimated 40,000 individuals, the Mongolian Gobi desert provides critical habitat for the largest remaining population of khulan (Buuveibaatar et al., 2016b). However, a substantial portion of the khulan’s range is under consideration for economic infrastructure development which may result in habitat deterioration, loss, and fragmentation (Batsaikhan et al., 2014; Ito et al., 2013). Khulan annual ranges vary regionally between 4500 and 70,000 km² (Kaczensky et al., 2011, 2006).

We conducted our study in the Great Gobi B Strictly Protected Area in the Dzungarian Gobi of southwestern Mongolia. The protected area covers 9000 km² plus a 5700 km² buffer zone, with elevations ranging from 1000 to 2900 m asl (Fig. 1). The protected area was established in 1975 to conserve semi-desert and desert ecosystems and their associated biodiversity, including several endangered ungulates such as about 5700 khulan and 5900 goitered gazelle *Gazella subgutturosa*, which are the two most abundant wild ungulates in the Dzungarian Gobi (Ransom et al., 2012). The area is bordered by the Altai Mountains in the north, and several high mountains (2500–2900 m) along the border with China in the south. Although the international border is fenced, the rest of the protected area is not surrounded or dissected by fences.

Most water sources are located in the foothills of the mountains, but underwater run-off channels also feed multiple springs in the plains and rolling hill country. Thus, the study area is characterized by sparsely distributed water sources, which in some places form oases, as well as ephemeral dry river beds and drainages. The study area has a continental climate with a mean annual temperature of -1.3°C , varying from $+35^{\circ}\text{C}$ in summer to -43°C in winter (Kaczensky et al., 2015a). The average annual precipitation is <100 mm with more than half of the precipitation occurring from June to August. Consequently, the growing season and greenest vegetation period (hereafter: vegetation period) lasts from June until mid-September.

Vegetation communities follow an elevational gradient (von Wehrden et al., 2006). High elevations (above 1800 m) are dominated by perennial grasses and sedges. Steep hills are almost devoid of vegetation with few perennial grasses. Intermediate elevations are characterized by desert-steppe with a high proportion of mixed shrub-grass communities, including shrubby *Salsola* spp. and *Anabasis* spp., the shrub *Haloxylon ammodendron* and *Stipa* spp. grasses. Depressions in the central part of the study area have unevenly scattered shrubs such as *H. ammodendron* and *Nitraria sibirica* (von Wehrden et al., 2006) interspersed with large patches of barren ground. Relatively high-productivity riparian vegetation communities are rare and restricted to larger oases and intermittently dry river valleys.

Due to its distance from population centers, the study area is subjected to relatively low human impact. In summer, human and livestock presence in the study area is minimal as herders move to the more productive summer pastures in the foothills and alpine meadows of the Altai Mountains.

2.2. Ground surveys

Between October 2003 and October 2010 Great Gobi B Strictly Protected Area staff conducted 33 ground-based surveys to monitor ungulates following a distance sampling approach (Kaczensky et al., 2015a). For this study, we used the 12 surveys conducted during the vegetation period (June–September) from 2004 to 2009.

A survey team consisted of four people (driver, observer, and two spotters with compasses) recruited from the park rangers and administration staff; driving speed was 40 km/h. Given the ruggedness of the topography (hills and shrub-covered depressions), we could not use a random or systematic survey design, but rather made use of an existing dirt track system. The survey consisted of 43 transect lines varying in length between 1.5 km and 32 km resulting in a total survey effort of 762 km. Surveys were attempted once a month (Table A.1), and the transects covered the entire protected area (Fig. 1).

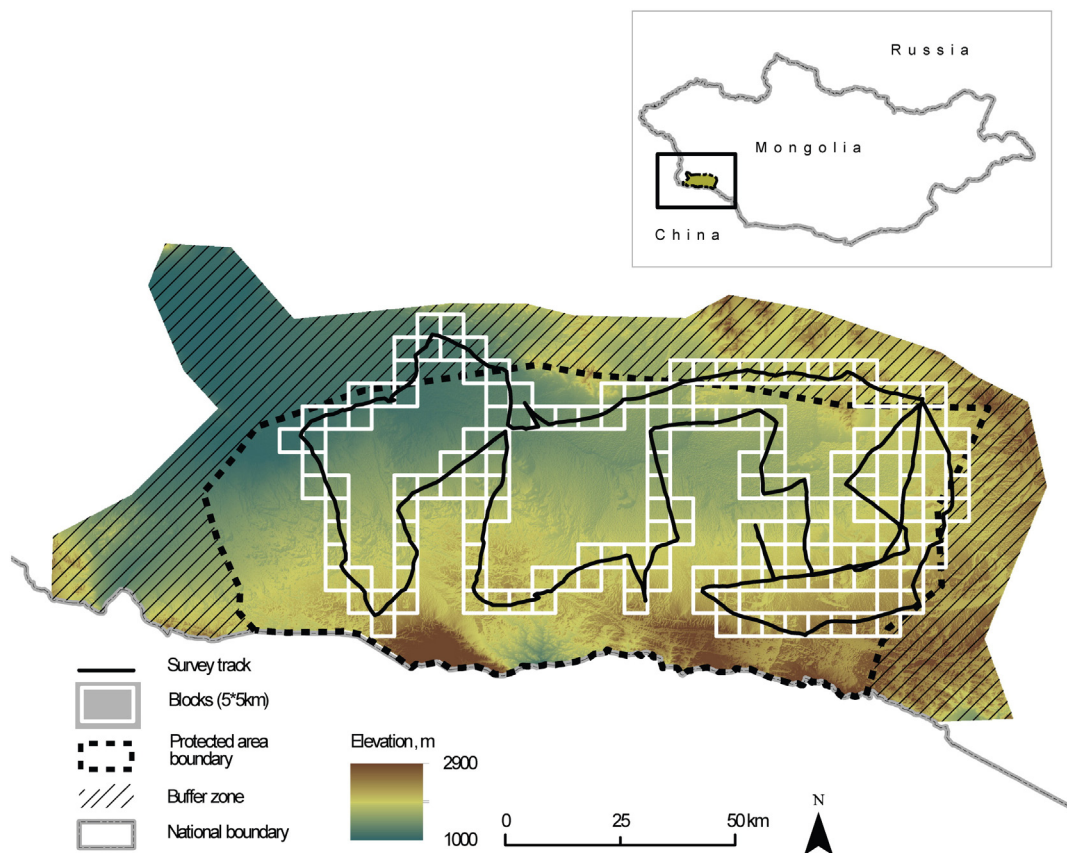


Fig. 1. The Great Gobi B strictly protected area and its buffer zone in the Dzungarian Gobi, Mongolia. Solid black lines indicate survey transects and white lines corresponding survey blocks that were used to summarize census data along the survey transects.

When a group of khulan or goitered gazelles was detected, observers recorded species, group size and their own location, observer distance to animal, and sighting angle using global positioning systems (GPS), and compass bearing respectively. Observers were repeatedly trained to visually estimate distances by placing people at intervals of 100, 500, 1000, 2000, 3000 and 5000 m. Species groups were defined as several animals standing or running in close proximity; no mixed species groups occur. Visibility in the study area is high due to extremely flat topography without steep depressions that would obstruct the observers view. We subsequently calculated the locations of detected khulan and goitered gazelle using geosphere library in R (Robert et al., 2016).

In total, we recorded 22,894 individual khulan in 723 groups and 5387 goitered gazelles in 1136 groups during summer surveys 2004–2009 (Table A.2). Most khulan groups consisted of <10 individuals, though we also recorded a few very large groups (> 500). The range in khulan group sizes varied from 1 to 2110 with a median of 64. This high variation in the abundance data makes models vulnerable to outliers and extreme values and we therefore converted khulan abundance into presence-absence data. Based on GPS tracking data of six khulan in the study area, the average daily displacement of khulan was 6 km. Given this khulan daily movement, we used 5 km² blocks to examine the relationship between khulan presence-absence and environmental covariates. To divide the survey tracks into 5km² blocks we used the 'XTools Pro' extension in ArcGIS 10.2 (Fig. 1). The length of the survey tracks varied between 714 and 877 km in response to varying dirt road conditions. Thus the total number of blocks varied from survey to survey (ranging between 153 and 191 blocks). A total of 295 khulan observed in 13 groups were excluded from analysis as their positions fell outside the 5 km² blocks. The final analysis is based on 710 groups (totaling 22,599 khulan) (Table A.2). Among individual surveys the number of blocks with khulan presence ranged from 17 to 53 (Table A.2);

blocks were assign absence (0) or presence (1) for khulan and goitered gazelles.

2.3. Dynamic and static covariates

We used static and dynamic environmental covariates in our model. We used the Normalized Difference Vegetation Index (NDVI) as a dynamic measure of vegetation productivity. NDVI is commonly used to monitor large-scale primary production dynamics over time and has proven a valuable index of resource availability and distribution of large herbivores (Pettorelli et al., 2011). Particularly in deserts and grasslands NDVI has been used as a direct indicator of forage availability and quality (Marshal et al., 2006). In our study region, the Gobi desert, NDVI has been shown as a good indicator of vegetation green up and indicator for spatiotemporal variability of foraging resources (Vandandorj et al., 2015).

For each of the survey periods, we used composite MODIS (moderate-resolution imaging spectroradiometer, available at <http://reverb.echo.nasa.gov/reverb>) NDVI images compiled over 16-day intervals at a spatial resolution of 500 × 500 m (Table A.1). For our analysis, we used the seven composites within each summer vegetation period from 2004 to 2009. As static environmental covariates, we used: (i) distance to water, calculated from 80 GPS points for water sources, (ii) a digital elevational model (DEM at 90-m resolution) acquired from Surface Radar Topography Mission (SRTM) data, and (iii) slope (°) calculated from the DEM using 'Spatial Analyst' extension in ArcGIS 10.2. We extracted the mean value of these variables for each survey block. We additionally included presence-absence data of goitered gazelle to test for potential interaction effects and classified survey blocks in protected area versus buffer zone to test for protection status in our model (Fig. 1).

2.4. Model development

We built logistic mixed (GLMM) habitat models based on the dynamic and static covariates to determine which variables have an effect on khulan habitat selection. To account for spatial autocorrelation, we calculated the proportion of neighboring blocks with khulan presence up to a Euclidean distance of 30 km from each block. To account for varying survey efforts among blocks we included the length of the survey track within each block. We standardized all covariates using a standard deviation of 1 and mean of 0.

To avoid sample asymmetry, we followed procedures in (Mueller et al., 2008) and randomly subsampled the blocks which had khulan absence to equal the number which had khulan presence for each survey. The model used khulan presence-absence as the response variable and included the twelve survey dates and the identifier of each 5 km² block as random effects. We used Restricted Maximum Likelihood to fit our model (REML, lme4 library in R) (Bates et al., 2015), and the Akaike information criterion (AIC) for model selection.

We subsequently built a reduced generalized linear model (GLM) by eliminating the presence-absence of goitered gazelle, the spatial autocovariate, and the length of the survey track from the full model. This reduced model was used to predict the probabilities of khulan occurrence and assess the habitat dynamics across the entire six years, including periods for which we did not have survey data (and thus could not calculate the eliminated variables). This model was also used for model validation with khulan GPS relocation data collected at time intervals different from the survey intervals.

2.5. Model validation

We validated predictions of the reduced model with an independent dataset of GPS locations at hourly intervals from six radio-collared khulan (3 males, 3 females; Fig. A.1).

Animals were marked in mid-summer 2009 and collars collected 1536 relocations (28 July – 29 September) during the period overlapping our 2009 model prediction layers. The data confirmed the extremely high mobility of khulan (Fig. A.1) documented previously (Kaczensky et al., 2008).

The khulan radio-collar locations occurred during four MODIS NDVI 16-day composite periods (see Table 2 in Results). By applying the reduced model, we predicted the probability of the khulan's occurrence for each of the four NDVI periods. From these surfaces we calculated the mean of all pixel values where actual khulan relocations occurred (see Fig. 2 in Results). To test whether this mean was significantly higher than expected by chance, we used random toroidal shifts (splancs library in R) (Rowlingson and Diggle, 1993) to offset the actual relocation patterns 1000 times within a rectangular bounding box which covers the entire study area and encompasses all relocations of khulan. For each random shift of the relocation pattern, we extracted the pixel values of the prediction map and calculated their mean. To determine the significance of our model, we compared 95% quantiles of mean probability of khulan occurrence for the shifted patterns to the mean of the probability of occurrence for the actual relocations of khulan. If the mean of actual relocations is above the 95% quantile of the average probability of the simulated data, this means that the

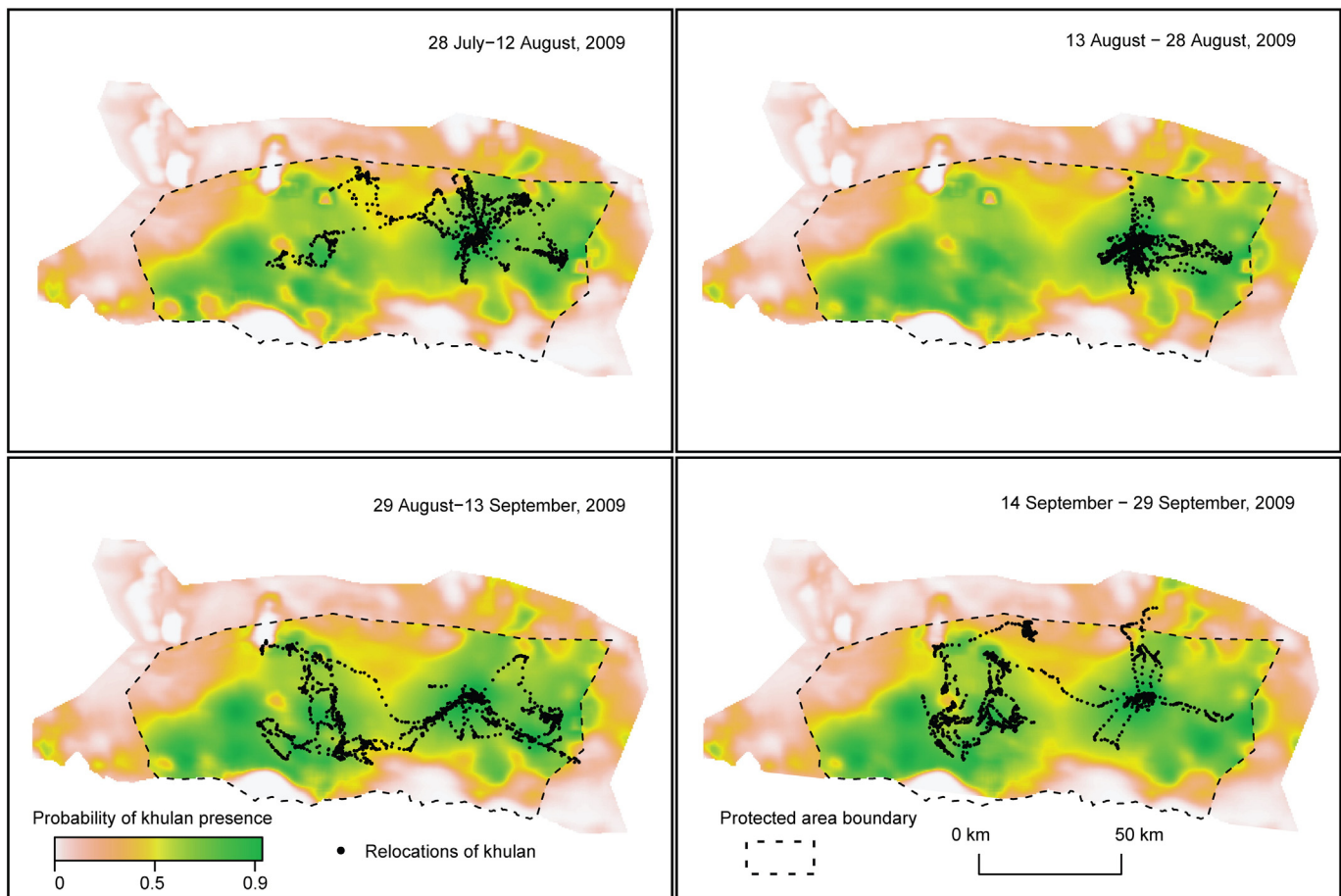


Fig. 2. Predicted probability maps of khulan occurrence (based on the models from the transect data) together with independently collected movement relocation data across four 16-day NDVI intervals in summer 2009. Black dots indicate movement relocations of khulan that correspond to a particular NDVI period. Note that the high degree of mobility of khulan within and between each 16-days interval. Each image contains 2304 relocations of six khulan sampled at hourly intervals.

model predicted khulan occurrence better than by chance, as the probability that the pattern could have emerged by chance is <0.05 .

2.6. Predictions of habitat dynamics

To assess khulan habitat dynamics for all summer vegetation periods over our six year study period, we acquired the 7 MODIS NDVI 16-day composites for each summer and year and applied the reduced model. We thus generated a total of 42 maps that showed a prediction of khulan occurrence for each NDVI period in each year (Fig. B.1). We then calculated the average and standard deviation across all prediction surfaces. The resulting maps allowed us to assess the degree of dynamics of summer foraging habitat within and among years.

3. Results

The logistic mixed model identified NDVI, elevation, distance to water, and protected area status as significant variables predicting the probability of khulan occurrence (Table 1). Slope was the only variable which was not significant in the model. NDVI and elevation were significant with their second-order polynomials, meaning that intermediate ranges of NDVI and elevation were preferred by khulan (Table 1). The coefficient for distance to water was negative indicating that khulan avoided distances too far from water. The model predicted that for median NDVI, elevation, and inside the protected area, khulan on average tended to stay within 21 km of water sources (Fig. B.2). In addition, our model suggested that there was a higher probability of khulan occurrence inside the protected area than in the buffer zone, and that khulan presence was positively related to goitered gazelle presence (Table 1).

We applied a reduced model using only the habitat covariates, and excluding the autocovariate and the length of survey track to predict khulan habitat (Table 1). The reduced model correctly predicted 74% (257 of 347) of the presence and 48% (166 of 347) of the absence blocks assuming 0.5 probability thresholds. The permutation test with independent movement data showed that in each of the four 16-day NDVI periods the actual relocations had a higher predicted probability of occurrence than the 95% quantile of the random shifts, and thus

demonstrated that our model predicted khulan significantly better than expected by chance (Table 2, Fig. 2).

Based on visual inspection of our 42 prediction maps we did not find significant spatiotemporal variability of summer foraging habitat between or within years (Fig. B.3 and Fig. B.4). The prediction maps showed a consistent pattern and we subsequently calculated a mean prediction map over the entire 6 years. The overall prediction map showed two large and more or less contiguous areas with a high probability of khulan occurrence which meet in the middle of the protected area and some areas of lower probability of khulan occurrence along the fringes in south and north-north-west (Fig. 3). Furthermore, the areas within the buffer zone have a much lower probability of khulan use than areas within the protected area (Fig. 3). A map of the standard deviation of our predictions showed that the main variability in the prediction surface was associated with water sources around larger oasis complexes and the foothills of the high mountains in the southwest (Fig. 4); this was the case both within and among years (Fig. B.5 and Fig. B.6). We examined the independent movement data in relation to these water sources and found that each khulan in average visited 10 (ranging between 5 and 13) different water sources during the summer season. These water sources were in average located 42 km apart from each other (ranging between 1.6 and 100 km, see Fig. A.1).

4. Discussion

4.1. Spatiotemporal dynamics of foraging habitat

We examined dynamics of foraging habitat of khulan in the Dzungarian Gobi during the summer vegetation period. We found that NDVI, elevation, distance to water, and protected area status, were all significant variables in predicting khulan occurrence. Based on NDVI, the only dynamic habitat variable in our model, our analysis showed that khulan selected for areas with intermediate values of NDVI, which helped to delineate the habitats where khulan occurred through the survey periods. Foraging resources were available rather continuously over two large regions within the protected area (Fig. 3). However, these habitats with intermediate values of NDVI did not vary at broad scales and thus prediction maps showed little variation and did not reveal spatiotemporal dynamics in khulan summer foraging habitat. While intermediate NDVI areas helped delineate broad scale foraging habitat and explained the broad regions where khulan occurred, they did not explain why khulan moved such great distances within these regions. This came as a surprise as researchers previously assumed that khulan foraging habitat is highly dynamic and unpredictable in space and time throughout the Gobi desert, and that this unpredictability drives the long-range movement of khulan within the vegetation period (Kaczensky et al., 2011, 2008).

In many other systems and ungulate species, spatiotemporal variability of foraging resources is indeed a main driver for nomadic movements and high mobility. This is especially true for resource-poor regions where animals often have to cope with great variability in the spatiotemporal distribution of ephemeral food resources (Gunn et al., 2008; Hancock et al., 2006; Mueller et al., 2011, 2008). However, our results revealed that khulan summer foraging habitat in the Dzungarian Gobi was rather predictable and showed very little spatiotemporal variability within and between years. In such case, there is little need for khulan to respond rapidly with long distance movements to changing forage resources and track them. This low degree of variation in khulan summer foraging habitat might be related to the fact that the vegetation in the Dzungarian Gobi consists in large parts of shrubland (a mix of small shrubs, forbs and grasses), whereas other studies that found greater variability in foraging habitat were primarily conducted in areas of herbaceous grassland (grasses and forbs) (Mueller et al., 2008; Singh et al., 2010a).

Dynamics of herbaceous and shrub vegetation in drylands are distinct due to different responses of these plants to precipitation in

Table 1

Logistic models predicting khulan presence in the Dzungarian Gobi during the vegetation period (June–September). Null deviance: 900.2 on 691 df; significance code: *, 0.05, **, 0.01, ***, 0.001. (a) Fixed effects of the full logistic mixed model, including a spatial autocovariate, a covariate for the presence of goitered gazelle, and the length of the transect track within each block: residual deviance: 771.4 on 681 df; AIC: 797.4. (b) Fixed effects for the reduced model that was used to create prediction maps excluding covariates for presence of goitered gazelle, auto-covariate and length of survey tracks: residual deviance: 848.59 on 686df, AIC: 864.59.

	Covariates	Estimate	SE	Z
(a) Full model	(Intercept)	-1.70	0.43	-3.87***
Dynamic covariate	NDVI	4.26	1.24	3.34***
	NDVI ²	-4.28	1.26	-3.37***
Static covariate	Log10 distance to water	-0.67	0.14	-4.54***
	Elevation	6.17	2.02	3.05**
	Elevation ²	-6.34	2.04	-3.10**
	Slope	-0.05	0.15	-0.36
	Boundary	1.26	0.44	2.86**
Accounting covariate	Presence of gazelle	0.97	0.20	4.67***
	Autocovariate	0.56	0.11	4.78***
	Length of transect	0.02	0.11	0.18
(b) Reduced model	(Intercept)	-30.52	5.90	-5.17***
Dynamic covariate	NDVI	23.91	6.08	3.93***
	NDVI ²	-11.85	2.99	-3.95***
Static covariate	Log10 distance to water	-1.72	0.32	-5.23***
	Elevation	32.61	7.83	4.16***
	Elevation ²	-10.55	2.61	-4.03***
	Slope	-0.16	0.10	-1.59
	Boundary	1.03	0.31	3.31***

Table 2
Comparison of predicted probability of occurrence between random shifts and actual khulan locations to validate the model. Actual movement data consisted of GPS relocations of six collared khulan ($N = 1536$ for each individual) across four 16-day NDVI intervals in summer 2009. Mean of 1000 random shifts of actual relocation patterns on prediction maps and its 95% quantile compared with the mean of actual relocations of khulan across four NDVI images. Note that in each of the four periods the mean of the probability of khulan occurrence from the actual relocations of khulan is higher than 95% quantiles of the random shifts.

16-day NDVI period	Mean of 1000 shifts	95% quantile of shifts	Mean of actual movement data
28 July–12 August, 2009	0.34	0.54	0.55
13 August–28 August, 2009	0.35	0.64	0.66
29 August–13 September, 2009	0.373	0.57	0.63
14 September–29 September, 2009	0.36	0.553	0.60

terms of growth and water-use patterns (Moreno-de las Heras et al., 2015). Herbaceous vegetation typically shows quick and intense growth pulses within a short term of rainfall and vegetation greenness is dynamic within a season. Conversely plant biomass and green-up phenology for shrub-dominated landscape are associated with longer-term precipitation patterns and vegetation greenness generally varies less over time (Moreno-de las Heras et al., 2015).

Studies conducted in herbaceous grasslands have previously found preference of herbivores for intermediate NDVI and have typically linked it to the forage maturation hypothesis, which predicts herbivores select an intermediate forage biomass to maximize net daily energy intake and is broadly referred to as a trade-off between forage quality and quantity (Hebblewhite et al., 2008; Mueller et al., 2008; Singh et al., 2010a, 2010b). In herbaceous grassland, variation in NDVI can be linked to different growth stages of the same vegetation types, and an intermediate range simply indicates a growth stage with the best trade-off between forage quantity and quality. In addition, most studies that found a preference for intermediate NDVI values (Hebblewhite et al., 2008; Mueller et al., 2008; Singh et al., 2010a, 2010b) have not only been conducted in herbaceous grasslands but also dealt with bovines, ruminants which tend to select for high forage quality rather than quantity. In contrast, the Dzungarian Gobi is shrub dominated and khulan are equids, non-ruminant hind-gut fermenters adapted to process large quantities of low quality forage (Duncan et al., 1990). Because in shrublands variation in NDVI is less related to growth stages, khulan preference for the intermediate NDVI values may be indicative of preferred habitat types, rather than be supportive of the forage maturation hypothesis. Vegetation communities with lower NDVI values are less suitable because they likely feature shrubs interspersed with barren ground and thus offer limited forage. Vegetation communities with

higher NDVI values are likely associated with riparian vegetation. Such riparian areas may be avoided as they are associated with a greater risk of predation and higher rates of insect harassment (Feh et al., 2001).

4.2. Water sources as alternative drivers of long-range movements

Our results suggest a rather predictable and contiguous foraging habitat for khulan in the Dzungarian Gobi. Consequently, the question remains why khulan exhibit long-range movements during summer. Previous studies have shown that equids are dependent on more or less daily access to water during summer, and that distance from water is an essential factor in habitat selection by wild equids (Giotto et al., 2015; Zhang et al., 2015). Our model showed that khulan avoided locations that were further than 21 km from water, and our prediction maps identified some variability at relatively small, localized spatial scales related to the location of water sources (Fig. 4). Thus, it may be the sparsely distributed and spatially patchy water sources which drive the long-range movements of khulan in the Dzungarian Gobi. Similar pattern have been found in African savannah elephants (*Loxodonta africana*) in Namibia's semi-arid system where mobility was induced by switching of water sources in order to access new foraging areas (Polansky et al., 2015). In the context of our study, khulan seem to be able use foraging areas up to a maximum of about 21 km of water sources, after which they are forced to either return to the previously visited water source or continue to a different one. The limited number of and large distance between water sources (e.g. no water source at all in the central part of the study area) thus modulate khulan use of the large contiguous foraging habitat. This was confirmed by our independent movement data that showed that each khulan indeed used many

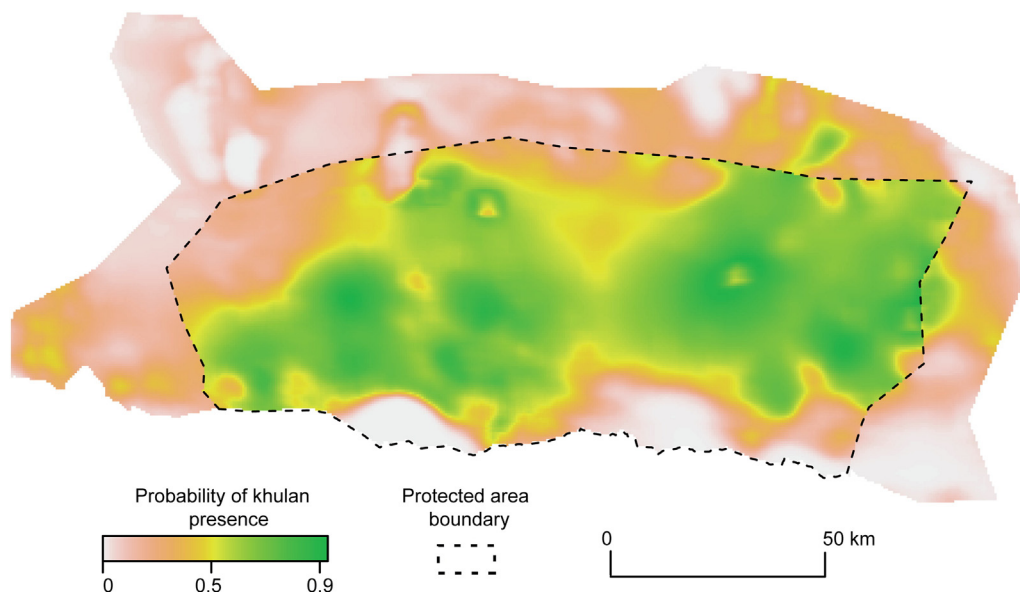


Fig. 3. Mean of 42 predicted probability maps of khulan presence during the vegetation period in the Dzungarian Gobi. Note that the probability of khulan presence in the protected area is generally higher than in the buffer zone area. See Fig. B.3–4 for mean prediction maps within and between years.

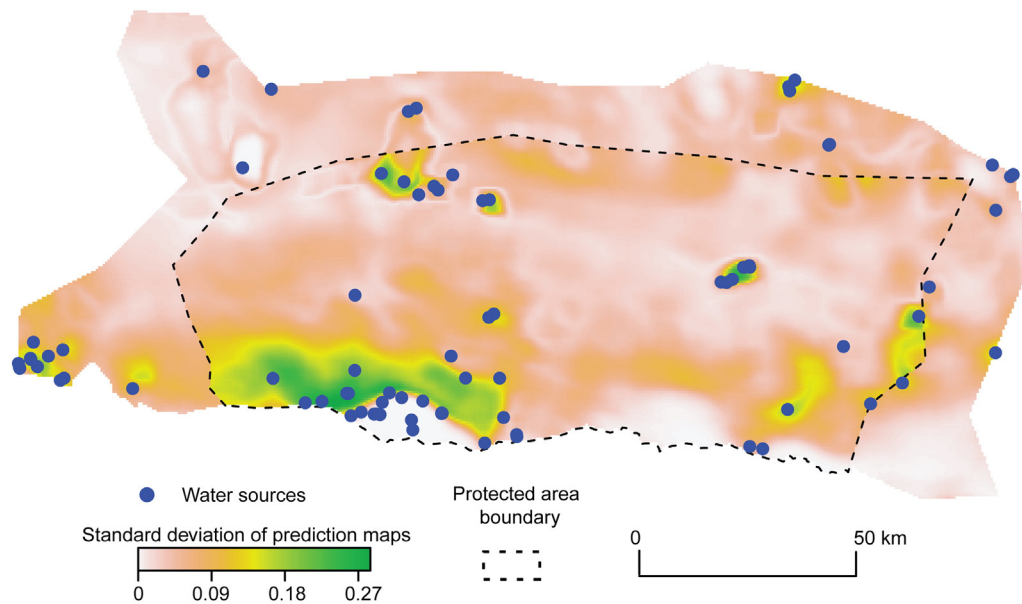


Fig. 4. Standard deviation of the 42 prediction maps of khulan presence and location of water sources. See Fig. B.5–6 for standard deviation maps within and between years.

different water sources that were located up to 100 km apart from each other.

Several explanations why khulan may have to switch between water sources are possible and may be inter-related. Since the areas around water sources were the most prone to habitat variability during summer periods, the attraction of different water sources to khulan can be expected to vary as well. Khulan preference may also be influenced by changes in water quality (e.g. salinity, contamination with animal urine and feces), micro-climate (e.g. wind which holds biting insects at bay), and presence or absence of other species (Zhang et al., 2015), including predators (Périquet et al., 2010; Valeix et al., 2009). In addition, vegetation adjacent to water sources that varies considerably with the water level and leads to the variability in NDVI may provide small scale but nevertheless valuable foraging. Variability of these small scale vegetation areas may be an additional driver for the long distance khulan movements. Disentangling these factors will be essential for fully understanding the long distance movements of khulan.

4.3. Non-habitat effects on khulan occurrence

In addition to the environmental habitat variables, we also found other effects on khulan occurrence such as protected area status and the presence of goitered gazelle. The probability of khulan occurrence was higher inside the protected area as compared to the buffer zone. This could be an effect of better protection of khulan against illegal hunting inside the protected area due to ranger presence, or a reaction to khulan preferring areas without herder camps and livestock presence as suggested previously for khulan and other ungulates in Mongolia (Kaczensky et al., 2011; Olson et al., 2011; Young et al., 2011). However, in the Dzungarian Gobi, herders and their livestock tend to leave the hot plains in summer and move into the foothills and mountains north of the protected area (von Wehrden et al., 2006).

Our results indicate that current protected area management is having a positive effect on khulan presence in the area. Therefore, strictly regulating livestock presence and controlling human activity within the protected area should remain a key focus of ranger patrols. Moreover, the occurrence of goitered gazelle was positively correlated with the occurrence of khulan. Unfortunately, detailed research on interactions between khulan and goitered gazelle does not exist. However, in other systems, mutual interactions with regard to feeding facilitation or predator avoidance among large mammalian herbivores has been

documented (Sinclair and Norton-Griffiths, 1982) and may also be relevant in the Gobi.

5. Conservation implications

Recent studies in movement ecology suggest that long-ranging species are increasingly threatened as a consequence of human land-use and climate change (Hobbs et al., 2008; Luo et al., 2015). Therefore, scientists have been focusing on understanding patterns and drivers of population-level long-distance movement and linking it with large-scale conservation efforts that attempt to maintain habitat connectivity for highly mobile species (Allen and Singh, 2016). Conservation management based on predictable animal movements, both migration and residence, is possible as we can anticipate connectivity among suitable habitats and resources and maintain ecological corridors between fragmented habitats. However, if a species has unpredictable movements or is nomadic it is more difficult to assess where ecological corridors need to be placed (Runge et al., 2014). Understanding which component of abiotic environmental variability is most important for promoting nomadic movement and how animals cope with resource dynamics and changing conditions is essential in order to identify the scale of conservation management and to develop a long-term conservation strategy for these species.

One key management implication of our study relates to the finding that long-range nomadic movements of large herbivores in resource poor landscapes are not always directly coupled with highly variable and unpredictable vegetation productivity. In the Dzungarian Gobi, sparsely distributed and patchy water sources, rather than dynamics of foraging habitats, appears to be the driver for long distance nomadic movement of khulan in summer. Our findings thus highlight that access to patchy key resources like water and connectivity among water bodies are critical for water-dependent grazers and nomadic species in arid and semi-arid, resource-poor landscapes. We are still only at the beginning of our understanding of what possible drivers under which circumstances drive nomadic, long-range movements in ungulates. Only a sound understanding of landscape scale drivers of long-range movements in khulan and other nomadic ungulates will allow us to minimize, mitigate, or offset the potential adverse effects of ongoing and future infrastructure development in drylands. Since khulan occurred more frequently inside than outside the protected area, this study also highlights successful landscape-scale conservation of the protected area that has been conserving wildlife since 1975. It encompasses many sparsely

distributed water sources from smaller springs to large oases. However, throughout the expanse of the entire Gobi in Mongolia, only about 27% of the khulan range are covered by protected areas (Buuveibaatar et al., 2016a) and future studies are needed to understand what makes khulan and other water-dependent wildlife chose certain water points and how wildlife use is influenced by environmental or anthropogenic factors throughout the expanse of the entire Gobi. Overall, conservation efforts to maintain nomadic herbivores should focus on functional connectivity among forage and other key resources such as water bodies and their extent. Future studies outside protected areas should focus on routing and frequency of animal movements among water bodies to provide deeper insights into where and how conservation measures could improve functional connectivity among resources.

Acknowledgments

Logistical and financial support was funded by the Austrian Science Foundation FWF project P14992 and P18624, the University of Veterinary Sciences in Vienna, and the Robert Bosch Foundation in Germany. Our special thanks to the administration of the Great Gobi B Strictly Protected Area, and the rangers who helped with logistics and carried out the long-term wildlife monitoring under harsh climate conditions in the Dzungarian Gobi. Without their field work, this study would not have been completed. We are grateful to S.R.B. King for assistance in editing English of this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.biocon.2016.10.021.

References

- Allen, A.M., Singh, N.J., 2016. Linking movement ecology with wildlife management and conservation. *Front. Ecol. Evol.* 3:1–13. <http://dx.doi.org/10.3389/fevo.2015.00155>.
- Avgar, T., Street, G., Fryxell, J.M., 2014. On the adaptive benefits of mammal migration. *NRC Res. Press* 92:481–490. <http://dx.doi.org/10.1139/cjz-2013-0076>.
- Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. *Fitting linear mixed-effects models using lme4*. *J. Stat. Softw.* 67, 1–48.
- Batsaikhan, N., Buuveibaatar, B., Chimed, B., Enkhuyaa, O., Galbrakh, D., Ganbaatar, O., Lkhagvasuren, B., Nandintsetseg, D., Berger, J., Calabrese, J.M., Edwards, A.E., Fagan, W.F., Fuller, T.K., Heiner, M., Ito, T.Y., Kaczensky, P., Leimgruber, P., Luschekina, A., Milner-Gulland, E.J., Mueller, T., Murray, M.G., Olson, K.A., Reading, R., Schaller, G.B., Stubbe, A., Stubbe, M., Walzer, C., Von Wehrden, H., Whitten, T., 2014. Conserving the World's finest grassland amidst ambitious National Development. *Conserv. Biol.*:1–4 <http://dx.doi.org/10.1111/cobi.12297>.
- Buuveibaatar, B., Mueller, T., Strindberg, S., Leimgruber, P., Kaczensky, P., Fuller, T.K., 2016a. Human activities negatively impact distribution of ungulates in the Mongolian Gobi. *Biol. Conserv.* 203:168–175. <http://dx.doi.org/10.1016/j.biocon.2016.09.013>.
- Buuveibaatar, B., Strindberg, S., Kaczensky, P., Payne, J., Chimeddorj, B., Naranbaatar, G., Amarsaikhan, S., Dashnyam, B., Munkhzul, T., Purevsuren, T., Hosack, D.A., Fuller, T.K., 2016b. Mongolian Gobi supports the world's largest populations of khulan *Equus hemionus* and goitered gazelles *Gazella subgutturosa*. *Oryx*:1–9 <http://dx.doi.org/10.1017/S0030605316000417>.
- Dean, W.R.J., 2004. *Nomadic Desert Birds*. Springer, Berlin.
- Dingle, H., Drake, V.A., 2007. What is migration? *Bioscience* 57:113. <http://dx.doi.org/10.1641/B570206>.
- Duncan, P., Foote, T.J., Gordon, I.J., Gakahu, C.G., Lloyd, M., 1990. Comparative nutrient extraction from forages by grazing bovines and equids: A test of the nutritional model of equid/bovid competition and coexistence. *Oecologia* 84:411–418. <http://dx.doi.org/10.1007/BF00329768>.
- Feh, C., Munkhtuya, B., Enkhhold, S., Sukhbaatar, T., 2001. Ecology and social structure of the Gobi khulan *Equus hemionus* subsp. in the Gobi B National Park. *Mongolia. Biol. Conserv.* 101:51–61. [http://dx.doi.org/10.1016/S0006-3207\(01\)00051-9](http://dx.doi.org/10.1016/S0006-3207(01)00051-9).
- Fryxell, J.M., Sinclair, A.R.E., 1988. Causes and consequences of migration by large herbivores. *Trends Ecol. Evol.* 3:237–241. [http://dx.doi.org/10.1016/0169-5347\(88\)90166-8](http://dx.doi.org/10.1016/0169-5347(88)90166-8).
- Fryxell, J.M., Wilmschurst, J.F., Sinclair, A.R.E., 2004. Predictive models of movement by serengeti grazers. *Ecology* 85:2429–2435. <http://dx.doi.org/10.1890/04-0147>.
- Giotto, N., Gerard, J.F., Ziv, A., Bouskila, A., Bar-David, S., 2015. Space-use patterns of the Asiatic wild ass (*Equus hemionus*): Complementary insights from displacement, recursion movement and habitat selection analyses. *PLoS One* 10:1–21. <http://dx.doi.org/10.1371/journal.pone.0143279>.
- Gunn, A., Poole, K.G., Wierzchowski, J., 2008. *A Geostatistical Analysis for the Patterns of Caribou Occupancy on the Bathurst Calving Grounds 1966–2007*. Indian and Northern Affairs Canada, Yellowknife, NWT.
- Hancock, P.A., Milner-Gulland, E.J., Keeling, M.J., 2006. Modelling the many-wrongs principle: The navigational advantages of aggregation in nomadic foragers. *J. Theor. Biol.* 240:302–310. <http://dx.doi.org/10.1016/j.jtbi.2005.09.019>.
- Hebblewhite, M., Merrill, E., McDermid, G., 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecol. Monogr.* 78:141–166. <http://dx.doi.org/10.1890/06-1708.1>.
- Hobbs, N.T., Galvin, K.A., Stokes, C.J., Lockett, J.M., Ash, A.J., Boone, R.B., Reid, R.S., Thornton, P.K., 2008. Fragmentation of rangelands: Implications for humans, animals, and landscapes. *Glob. Environ. Chang.* 18:776–785. <http://dx.doi.org/10.1016/j.gloenvcha.2008.07.011>.
- Holdo, R.M., Holt, R.D., Fryxell, J.M., 2009. Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *Am. Nat.* 173:431–445. <http://dx.doi.org/10.1086/597229>.
- Ito, T.Y., Lhagvasuren, B., Tsunekawa, A., Shinoda, M., Takatsuki, S., Buuveibaatar, B., Chimeddorj, B., 2013. Fragmentation of the habitat of wild ungulates by anthropogenic barriers in Mongolia. *PLoS One* 8:1–9. <http://dx.doi.org/10.1371/journal.pone.0056995>.
- Jacoby, D.M.P., Freeman, R., 2016. Emerging network-based tools in movement ecology. *Trends Ecol. Evol.* 31:301–314. <http://dx.doi.org/10.1016/j.tree.2016.01.011>.
- Janis, C., 1976. The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. *Evolution (N. Y.)* 30:757–774. <http://dx.doi.org/10.2307/2407816>.
- Jonzén, N., Knudsen, E., 2011. Uncertainty and predictability: the niches of migrants and nomads. In: Milner-Gulland, E.J., Fryxell, J.M., Sinclair, A.R.E. (Eds.), *Animal Migration: A Synthesis*. Oxford Univ. Press, pp. 91–109.
- Kaczensky, P., Ganbaatar, O., Altansukh, N., Enksaikhan, N., Kramer-Schadt, S., 2015a. Monitoring of Khulans and goitered gazelles in the Mongolian Gobi – potential and limitations of ground based line transects. *Open Ecol. J.* 8:92–110. <http://dx.doi.org/10.2174/1874213001508010092>.
- Kaczensky, P., Ganbaatar, O., von Wehrden, H., Walzer, C., 2008. Resource selection by sympatric wild equids in the Mongolian Gobi. *J. Appl. Ecol.* 45:1762–1769. <http://dx.doi.org/10.1111/j.1365-2664.2007.0>
- Kaczensky, P., Kuehn, R., Lhagvasuren, B., Pietsch, S., Yang, W., Walzer, C., 2011. Connectivity of the Asiatic wild ass population in the Mongolian Gobi. *Biol. Conserv.* 144:920–929. <http://dx.doi.org/10.1016/j.biocon.2010.12.013>.
- Kaczensky, P., Lkhagvasuren, B., Pereladova, O., Hemami, M., Bouskila, A., 2015b. *Equus hemionus*. The IUCN Red List of Threatened Species (doi:e.T7951A45171204).
- Kaczensky, P., Sheehy, D.P., Johnson, D.E., Walzer, C., Lkhagvasuren, B., Sheehy, C.M., 2006. Room to Roam? The Threat to Khulan (Wild Ass) from Human Intrusion. *Mongolia Discussion Papers*. World Bank, Washington, D.C: World Bank. <http://documents.worldbank.org/curated/en/559701468060257075/Mongolia-Room-to-roam-the-threat-to-Khulan-wild-ass-from->
- Luo, Z., Jiang, Z., Tang, S., 2015. Impacts of climate change on distributions and diversity of ungulates on the Tibetan plateau. *Ecol. Appl.* 25:24–38. <http://dx.doi.org/10.1890/151499.1>.
- Marshall, J.P., Bleich, V.C., Krausman, P.R., Reed, M.L., Andrew, N.G., 2006. Factors affecting habitat use and distribution of desert mule deer in an arid environment. *Wildl. Soc. Bull.* 34:609–619. [http://dx.doi.org/10.2193/0091-7648\(2006\)34\(609:FAHUAD\)2.0.CO;2](http://dx.doi.org/10.2193/0091-7648(2006)34(609:FAHUAD)2.0.CO;2).
- Moreno-de las Heras, M., Díaz-Sierra, R., Turnbull, L., Wainwright, J., 2015. Assessing vegetation structure and ANPP dynamics in a grassland–shrubland Chihuahuan ecotone using NDVI–rainfall relationships. *Biogeosciences* 12:2907–2925. <http://dx.doi.org/10.5194/bg-12-2907-2015>.
- Mueller, T., Fagan, W.F., 2008. Search and navigation in dynamic environments – from individual behaviours to population distributions. *Oikos* 117:654–664. <http://dx.doi.org/10.1111/j.2008.0030-1299.16291.x>.
- Mueller, T., Olson, K.A., Dressler, G., Leimgruber, P., Fuller, T.K., Nicolson, C., Novaro, A.J., Bolgeri, M.J., Watters, D., Destefano, S., Calabrese, J.M., Fagan, W.F., 2011. How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. *Glob. Ecol. Biogeogr.* 20:683–694. <http://dx.doi.org/10.1111/j.1466-8238.2010.00638.x>.
- Mueller, T., Olson, K.A., Fuller, T.K., Schaller, R., Murray, M.G., Leimgruber, P., 2008. In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *J. Appl. Ecol.* 45:649–658. <http://dx.doi.org/10.1111/j.1365-2664.2007.01371.x>.
- Olson, K.A., Mueller, T., Kerby, J.T., Bolortsetseg, S., Leimgruber, P., Nicolson, C.R., Fuller, T.K., 2011. Death by a thousand huts? Effects of household presence on density and distribution of Mongolian gazelles. *Conserv. Lett.* 4:304–312. <http://dx.doi.org/10.1111/j.1755-263X.2011.00180.x>.
- Périquet, S., Valeix, M., Loveridge, A.J., Madzikanda, H., Macdonald, D.W., Fritz, H., 2010. Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. *Anim. Behav.* 79:665–671. <http://dx.doi.org/10.1016/j.anbehav.2009.12.016>.
- Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., Kausrud, K., 2011. The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. *Clim. Res.* 46:15–27. <http://dx.doi.org/10.3354/cr00936>.
- Polansky, L., Kilian, W., Wittemyer, G., Polansky, L., 2015. Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state – space models. *Proc. R. Soc. B* 282. <http://dx.doi.org/10.1098/rspb.2014.3042>.
- Ransom, J.L., Kaczensky, P., Lubow, B.C., Ganbaatar, O., Altansukh, N., 2012. A collaborative approach for estimating terrestrial wildlife abundance. *Biol. Conserv.* 153:219–226. <http://dx.doi.org/10.1016/j.biocon.2012.05.006>.
- Robert, A., Hijmans, J., Williams, E., Vennes, C., Hijmans, M.R.J., 2016. *Package “Geosphere”*.
- Roshier, D.A., Doerr, V.A.J., Doerr, E.D., 2008. Animal movement in dynamic landscapes: Interaction between behavioural strategies and resource distributions. *Oecologia* 156:465–477. <http://dx.doi.org/10.1007/s00442-008-0987-0>.

- Rowlingson, B.S., Diggle, P.J., 1993. SPLANCS: spatial point pattern analysis code in S-plus. *Comput. Geosci.* 19:627–655. [http://dx.doi.org/10.1016/0098-3004\(93\)90099-Q](http://dx.doi.org/10.1016/0098-3004(93)90099-Q).
- Runge, C.A., Martin, T.G., Possingham, H.P., Willis, S.G., Fuller, R.A., 2014. Conserving mobile species. *Front. Ecol. Environ.* 12:395–402. <http://dx.doi.org/10.1890/130237>.
- Sinclair, A.R.E., Norton-Griffiths, M., 1982. Does competition or facilitation regulate migrant ungulate population in the Serengeti? A test of hypotheses. *Oecologia* 53, 364–369.
- Singh, N.J., Börger, L., Dettki, H., Bunnefeld, N., Ericsson, G., 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecol. Appl.* 22:2007–2020. <http://dx.doi.org/10.2307/1942049>.
- Singh, N.J., Grachev, I.A., Bekenov, A.B., Milner-Gulland, E.J., 2010a. Tracking greenery across a latitudinal gradient in central Asia - the migration of the Saiga antelope. *Divers. Distrib.* 16:663–675. <http://dx.doi.org/10.1111/j.1472-4642.2010.00671.x>.
- Singh, N.J., Yoccoz, N.G., Lecomte, N., Côté, S.D., Fox, J.L., 2010b. Scale and selection of habitat and resources: Tibetan argali (*Ovis ammon hodgsoni*) in high-altitude rangelands. *Can. J. Zool.* 88:436–447. <http://dx.doi.org/10.1139/Z10-015>.
- Taillon, J., Festa-Bianchet, M., Côté, S.D., 2012. Shifting targets in the tundra: protection of migratory caribou calving grounds must account for spatial changes over time. *Biol. Conserv.* 147:163–173. <http://dx.doi.org/10.1016/j.biocon.2011.12.027>.
- Valeix, M., Loveridge, A.J., Chammille-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., Macdonald, D.W., 2009. Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology* 90:23–30. <http://dx.doi.org/10.1890/08-0606.1>.
- Vandandorj, S., Gantsetseg, B., Boldgiv, B., 2015. Spatial and temporal variability in vegetation cover of Mongolia and its implications. *J. Arid. Land.* <http://dx.doi.org/10.1007/s40333-015-0001-8>.
- von Wehrden, H., Hanspach, J., Kaczensky, P., Fischer, J., Wesche, K., 2012. Global assessment of the non-equilibrium concept in rangelands. *Ecol. Appl.* 22:393–399. <http://dx.doi.org/10.1890/07-1650.1>.
- von Wehrden, H., Wesche, K., Tungalag, R., 2006. Plant communities of the great Gobi B strictly protected area, Mongolia. *J. Biol. Sci.* 4, 63–66.
- Xu, W., Xia, C., Yang, W., Blank, D.A., Qiao, J., Liu, W., 2012. Seasonal diet of khulan (*Equidae*) in northern Xinjiang, China. *Ital. J. Zool.* 79:92–99. <http://dx.doi.org/10.1080/11250003.2011.620635>.
- Young, J.K., Olson, K.A., Reading, R.P., Amgalanbaatar, S., Berger, J., 2011. Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. *Bioscience* 61:125–132. <http://dx.doi.org/10.1525/bio.2011.61.2.7>.
- Zhang, Y., Cao, Q.S., Rubenstein, D.L., Zang, S., Songer, M., Leimgruber, P., Chu, H., Cao, J., Li, K., Hu, D., 2015. Water use patterns of sympatric Przewalski's horse and khulan: interspecific comparison reveals niche differences. *PLoS One* 10:1–17. <http://dx.doi.org/10.1371/journal.pone.0132094>.