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In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity

THOMAS MUELLER*, KIRK A. OLSON†‡, TODD K. FULLER†,
GEORGE B. SCHALLER‡, MARTYN G. MURRAY§ and
PETER LEIMGRUBER

*Smithsonian Institution, National Zoological Park, Conservation & Research Center, 1500 Remount Road, Front Royal, VA 22630, USA; *Behaviour, Ecology, Evolution, and Systematics Program, University of Maryland, College Park, MD 20742, USA; †Department of Natural Resources Conservation, 160 Holdsworth Way, University of Massachusetts, Amherst, MA 01003-9285, USA; ‡Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, USA; §Institute of Evolutionary Biology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, UK*

Summary

1. Temporal variability in habitat suitability has important conservation and ecological implications. In grasslands, changes in resource availability can occur at broad spatial scales and enlarge area requirements of ungulate populations, which increases their vulnerability to habitat loss and fragmentation. Understanding and predicting these dynamics, although critical, has received little attention so far.

2. We investigated habitat dynamics for Mongolian gazelles (*Procapra gutturosa* Pallas) in the eastern steppes of Mongolia. We quantified the distribution of gazelles at four different time periods and tracked primary productivity using Normalized Difference Vegetation Index (NDVI) data from satellite imagery.

3. A second-order logistic model showed that NDVI was an efficient predictor of gazelle presence. We tested the predictive power of the model with independent data from a gazelle telemetry study: 85% of all relocations were found within the predicted area.

4. Gazelles preferred an intermediate range of vegetation productivity, presumably facing quality quantity trade-offs where areas with low NDVI are limited by low ingestion rates, and areas with high NDVI are limited by the low digestibility of mature forage.

5. Spatiotemporal variation of gazelle habitat areas was high. Only 15% of the study area was consistently gazelle habitat throughout all survey periods, indicating that gazelles need to range over vast areas in search of food. Only 1% of the gazelle habitats were consistently located inside protected areas.

6. *Synthesis and applications.* Habitat variability in grasslands often leads to area requirements of ungulates that prevent effective conservation within single protected areas. They require landscape-level management plans, but dynamic habitat predictions to inform such plans are difficult to implement and are often unavailable. We showed that satellite estimates of vegetation productivity can be used successfully to generate dynamic habitat models in landscapes with highly variable resources, and demonstrated that intermediate NDVI values were critical to predict occurrence of Mongolian gazelles.

Key-words: dynamic landscape, forage maturation, grassland, migration, Mongolia, NDVI, nomadism, ungulate, *Procapra gutturosa*

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Correspondence: Thomas Mueller. E-mail: muellert@gmail.com

Introduction

Mongolian gazelles (*Procapra gutturosa* Pallas) are the dominant wild large herbivore in Mongolia's eastern steppe, one of the largest remaining grasslands in the temperate zone (Schaller 1998b; Olson *et al.* 2005a). While these gregarious animals still roam Mongolian grasslands in large numbers (at least 800 000–900 000 animals in the study region; Olson *et al.* 2005a), the species has experienced a major reduction in range during the past century, and is further threatened by continued habitat loss, fragmentation and excessive hunting (Lhagvasuren & Milner-Gulland 1997; Reading *et al.* 1998). Although individuals or small groups are found across a wider geographical range, higher concentrations of this gazelle species are now limited to the eastern steppe (Lhagvasuren & Milner-Gulland 1997; Wang *et al.* 1997; Reading *et al.* 1998; Sneath 1998).

Movements of Mongolian gazelles occur year-round over large distances, with only short interruptions throughout calving time (Lhagvasuren & Milner-Gulland 1997; Schaller 1998b; Olson *et al.* 2005b; Ito *et al.* 2006). They appear to be nomadic and lack regularity (K.A.O. and co-workers, unpublished data), yet their paths and patterns are little understood (Ito *et al.* 2006). Quantifying the spatiotemporal heterogeneity of gazelle habitat use will be helpful in better understanding the species' area needs and developing much-needed integrative and landscape-level conservation strategies.

Modelling habitat use in grasslands is particularly challenging, as these ecosystems are characterized by a continuously varying landscape (Fernandez-Gimenez & Allen-Diaz 1999; Fryxell *et al.* 2005). Most existing habitat models are static, and only recently have habitat modelling studies started to focus on dynamic landscapes (Hanski 1999; Higgins *et al.* 2000; Wahlberg, Klemetti & Hanski 2002). In addition, many of these models focus either on metapopulation theory (Keymer *et al.* 2000; DeWoody, Feng & Swihart 2005; Xu *et al.* 2006) or on modelling habitats in ecosystems that are dynamic over longer time frames (e.g. forests: Akcakaya *et al.* 2004; Verheyen *et al.* 2004; Wintle *et al.* 2005). Short-term and broad-scale changes that are common in grasslands are difficult to model, as data on environmental covariates are usually difficult to acquire at similar temporal and spatial scales (Fryxell, Wilmshurst & Sinclair 2004). However, satellite-borne sensors allow measurement of vegetation productivity, a key variable indicating resource availability for grassland ungulates, across broad spatial scales and at relatively frequent temporal intervals (Reed *et al.* 1994; Huete *et al.* 2002). Normalized Difference Vegetation Index (NDVI) is a satellite-based vegetation estimator that has consistently shown close correlations with vegetation productivity in a diverse range of ecosystems (reviewed by Pettorelli *et al.* 2005) and, specifically in grasslands, with total biomass as well (Kawamura *et al.* 2003, 2005a).

Numerous studies already demonstrate that NDVI is a useful tool to predict habitats for ungulates in grasslands. It has been used successfully to test the relationship between ungulate diversity and plant productivity across the African continent (Baird 2001) and to evaluate ungulate habitat use in the Kalahari (Verlinden & Masogo 1997), rangeland stocking rates in Argentina (Oesterheld, DiBella & Kerdiles 1998), wildebeest (*Connochaetes taurinus*) population declines and movements in Kenya (Serneels & Lambin 2001; Musiega & Kazadi 2004), distribution of impala (*Aepyceros melampus*) in Botswana (Van Bommel *et al.* 2006), and also to characterize habitat use of Mongolian gazelles (Leimgruber *et al.* 2001; Ito *et al.* 2005, 2006). However, none of these studies used detailed and broad-scale distribution data of a species to identify preferred ranges of NDVI and to make predictions on habitat occupancy when availability changes.

We used NDVI satellite imagery to predict gazelle occurrence data from four extensive surveys across the eastern steppes. Specifically, we sought to reveal whether gazelles select for a specific range of productivity. Instead of assuming a monotonic relationship between NDVI and resource availability, we tested predictions with regard to forage maturation: While areas with too little vegetation may not provide sufficient ingestion rates, most grasses decline considerably in nutritional quality as they grow (Van Soest 1994). Mature forage may provide high vegetation productivity, yet few resources to gazelles as digestion rates are reduced (Fryxell 1991; Murray & Illius 1996; Wilmshurst *et al.* 1999; Wilmshurst, Fryxell & Bergman 2000; Bergman *et al.* 2001). As the landscape in the eastern steppe features almost no trees and few shrubs, it is likely that, in general, high NDVI values are associated with higher, more mature and therefore less nutritious grasses, which has been shown elsewhere (Payero *et al.* 2004; Kawamura *et al.* 2005a, 2005b). An intermediate range of NDVI, allowing for sufficient forage quantity as well as quality, may provide most resources to gazelles, and might be a useful tool to delineate habitats and reveal area needs of Mongolian gazelles.

Methods

STUDY AREA

Mongolia's eastern steppe is one of the world's largest remaining intact grasslands and harbours the greatest concentration of wild ungulates in Asia (Schaller 1998b). Neighbouring grasslands to the south in Inner Mongolia, China are severely overgrazed and degraded (Jiang *et al.* 2003a) and have fewer wild ungulates (Wang *et al.* 1997). The eastern steppe is characterized by gently rolling hills, broad, flat plains (altitude 600–1100 m asl) and sparsely scattered small ponds and springs. The region's major river, the Kherlen, bisects the steppe from west to east. The climate is continental with long, cold winters (January mean = –26 °C) and short, warm summers (July mean = 19 °C). Warm-season precipitation occurs mainly during July and August, and overall precipitation is generally between 200 and 300 mm

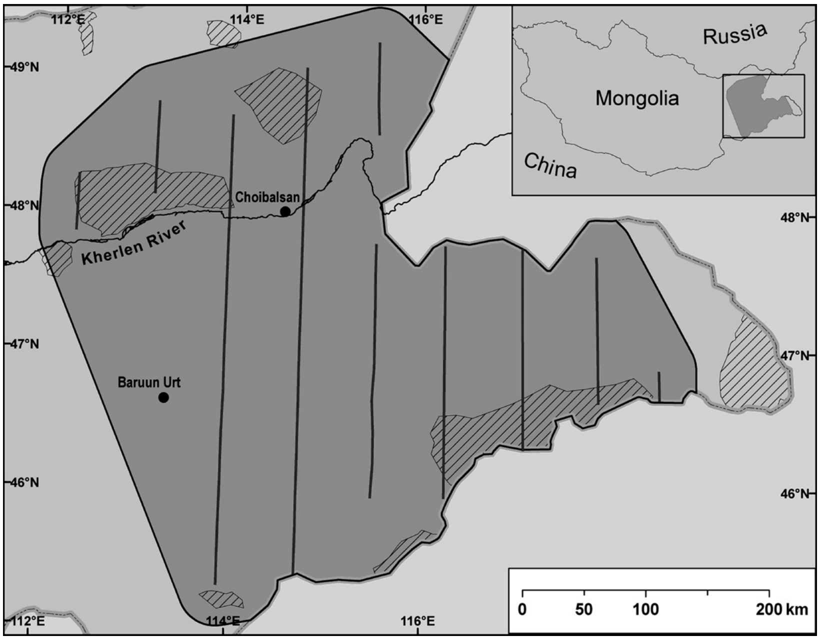

Fig. 1. Mongolia's eastern steppes with study area in dark grey and survey transects shown as straight lines. Hatched areas indicate protected areas and wildlife reserves.

Table 1. Dates and distances of gazelle surveys and matching periods for Normalized Difference Vegetation Index (NDVI) composites

			Gazelle survey		NDVI composite	
Year	Season	Distance (km)	Start	End	Start	End
2000	Spring	1286	05–15	06–02	05–25	06–09
2001	Autumn	1252	09–27	10–10	09–30	10–15
2002	Spring	1591	05–19	06–08	05–25	06–09
2002	Autumn	1454	08–26	09–06	08–29	09–13
2001	Summer	Telemetry	07–15	07–30	07–12	07–27

year^{-1} (Gunin *et al.* 2000). Onset of green-up during the 1980s occurred from late May to early June (Lee *et al.* 2002; Yu *et al.* 2003). Dominant soil types are characterized as sandy loamy chestnut soils with localized sites of highly salinized soil (Gunin *et al.* 2000). The steppe is homogeneous in both its topography and vegetation. Vegetation is mostly dominated by grasses such as *Stipa* spp. and *Leymus* spp. as well as the forbs *Artemesia* spp. and *Allium* spp.; a few shrubs (*Caragana* spp.) are present and trees are rare, occurring in isolated pockets (Gunin *et al.* 2000; Tong *et al.* 2004). A narrow band of woody vegetation consisting of mostly willow (*Salix* spp.) exists along the flood plain of the Kherlen. Semi-nomadic pastoralists live throughout the region at some of the lowest densities in the country (0·7 km^{-2}; Milner-Gulland & Lhagvasuren 1998).

GAZELLE SURVEY AND RADIO TRACKING

We used gazelle locations in a 150 000-km^2 area during four surveys conducted by Olson *et al.* (2005a), adding data from north of the Kherlen River (Fig. 1). The survey protocol followed guidelines recommended by Buckland *et al.* (2001). Transect locations were spaced at 60-km intervals running north–south, and driving speeds were kept between 25 and 35 km h^{-1} (Olson et al. 2005a; Fig. 1). Transect locations remained the same for all surveys and ranged between 50 and 350 km in length, with six to seven transects per survey. The total distance covered for these surveys was 5169 km (Table 1). Gazelle group locations were recorded using global positioning systems (GPS) (Olson *et al.* 2005a). Spring surveys (2000, 2002) were conducted during late May to mid-June; autumn surveys (2001, 2002) were conducted from late August to early October (Table 1). For model validation, we used locations obtained from radio-collared calves in 2001 (Olson *et al.* 2005b). Calving aggregations can be detected in late June (Olson *et al.* 2005b). By walking through the calving region we were able to detect newborn, hiding calves which were captured and fitted with an expanding VHF radio transmitter (Olson *et al.* 2005b). Movements of marked calves were monitored from the ground by vehicles over the course of the year. When a marked gazelle was detected, Olson *et al.* (2005b) visually confirmed the group location and recorded the position with a GPS.

REMOTE SENSING, GIS AND MODEL DEVELOPMENT

To develop a habitat model based on vegetation productivity, we used NDVI data acquired by the moderate-resolution imaging spectroradiometer (MODIS) on board the TERRA satellite. For each of the survey periods, we obtained a 16-day NDVI composite in 500-m resolution from NASA's Earth Observing System Gateway (http://edcimswww.cr.usgs.gov/pub/imswelcome; for details see Huete *et al.* 2002) and re-projected the data to Transverse Mercator (UTM zone 50 N; Table 1). We matched gazelle and satellite data by subdividing each transect line into 1 × 5-km blocks and determined the mean NDVI as well as gazelle presence or absence for each block. The 1 km width of these blocks approximated the effective strip width for detection of gazelles (Buckland *et al.* 2001; Olson *et al.* 2005a); given the high mobility of gazelles, finer scales than 5 km seemed to be inappropriate. Mongolian gazelles move an average of about 9 km per day (K.A.O. and co-workers, unpublished data), and even at the coarse 5-km scale, an asymmetrical sample distribution of presence and absence data is probably caused by many false negatives (Tyre *et al.* 2003). To eliminate sample asymmetry (more absent than present data) and balance statistical analysis we randomly subsampled the absence blocks to equal the number of presence samples in each survey. We equalized phenological differences in total vegetation productivity by linearly normalizing the NDVI data for each survey using minimum–maximum scaling.

We used maximum likelihood and the Akaike information criterion (AIC) for model selection and penalized quasi-likelihood (PQL, lme4 library in R; Bates 2005; R Development Core Team 2006) to implement second-order autologistic generalized linear mixed models predicting gazelle presence/absence based on NDVI (Boyce & McDonald 1999; Manly *et al.* 2002; Boyce *et al.* 2003; Bates 2005). To test predictions regarding forage maturation-related quantity–quality trade-offs, we used the first- and second-order polynomial of the scaled NDVI variable. The first-order term tested for low probability of gazelle occurrence at low productivity areas (quantity limitation of forage). A significant negative coefficient of the second-order polynomial would predict low probability of occurrence at high-productivity areas (quality limitation of mature forage). However, it is not just the relative range of NDVI that may be important, but also interactions with absolute resource amount, that is, the variation in phenology between surveys. This was considered by including the median of the non-scaled NDVI data from each survey into the model and testing for interaction effects with the relative (minimum–maximum scaled) NDVI data. Between seasons, differences in vegetation quality may occur, and we incorporated seasons (autumn vs. spring) as a fixed factor in the analysis. Additionally, we explicitly modelled spatial autocorrelation (Augustin, Mugglestone & Buckland 1996) by including as an autocovariate the number (0, 1 or 2) of neighbouring blocks (the next 5-km block to the north and to the south) where gazelles did occur. Based on AIC, we excluded effects that did not significantly improve the model in any factor combination. As observations were grouped in four different surveys, those were included as a random effect in the final minimum adequate model. As a predictive tool to classify new NDVI scenes in gazelle presence and absence areas without prior information about gazelle occurrence in adjacent areas, we calculated a reduced model excluding the auto-regressive term.

While probabilities are generally more informative and were used for model testing, we believe thresholds are a helpful tool in conservation management and for simple and applied assessments, as intended in this study. Comparison of predicted values and actual prevalence (Vaughan & Ormerod 2005) suggested 0·5 probability thresholds as an appropriate measure to classify NDVI scenes into predicted gazelle presence/absence areas and explore omission as well as commission errors.

We tested the reduced model with an independent data set from the telemetry study. We selected all relocations of gazelle groups (≥ two animals) in the second half of July 2001 (67 group relocations of 33 radio-tagged animals) and acquired a MODIS NDVI 16-day composite for the according time lag (Table 1). At this time of year, calves already follow the generally mixed herds and are representative for both male and female habitat selection. The NDVI data were processed following the same procedures as were applied during model development. By applying our model to this NDVI scene, we calculated a surface predicting the probability of gazelle occurrence throughout the eastern steppe. From this surface we calculated the mean of all pixel values where actual relocations occurred. To test whether this mean was significantly higher than expected by chance, we simulated 1000 random toroidal shifts (Fortin & Dale 2005) of the relocation pattern within a boundary box (a minimum rectangle of ≈18 000 km^2 encompassing all relocations). For each shift, we extracted the pixel values of the prediction surface and calculated their mean. We determined the significance of our model by counting how many of the simulated patterns had a higher average probability of occurrence than the mean calculated from actual gazelle relocations. We also created a minimum convex polygon (excluding areas in China) derived from all gazelle telemetry observations obtained during the duration of the entire telemetry study from June 2001 to January 2002 (telemetry area, see Fig. 4). We used 0·5 probability thresholds to classify the surface into predicted gazelle presence vs. absence areas. We qualitatively compared the proportion of available habitats with selected habitats. However, we did not test these findings due to clumping and non-independence of the relocation data.

Table 2. Fixed effects of logistic mixed models predicting gazelle occurrence with Normalized Difference Vegetation Index (NDVI) across four survey periods

	Coefficient	Estimate	SE	*Z*	Deviance
A	(Intercept)	–2·55	0·42	–6·11***	1·59
	NDVI	6·64	1·88	3·53***	7·44
	NDVI^2	–6·58	2·00	–3·29***	25·65
	AutoCov	1·71	0·15	11·60***	183·63
B	(Intercept)	–1·91	0·36	–5·27***	1·59
	NDVI	8·77	1·66	5·29***	7·44
	NDVI^2	–8·33	1·75	–4·76***	25·65

Estimate for variance of the random effect (survey period) was effectively zero. Null deviance: 884·46 on 637 df; significance code: ***, 0·001.

A, Full model including spatial autocovariance (AutoCov); residual deviance: 666·14, Akaike information criterion (AIC): 674, estimated scale: 1·02.

B, Reduced model; residual deviance: 849·77, AIC: 858, estimated scale: 1·00.

Results

Vegetation productivity approximated by NDVI was an important factor shaping gazelle habitat use. The auto-logistic model relating gazelle presence/absence to NDVI showed that gazelles preferred an intermediate range of vegetation productivity; despite a strong positive spatial autocorrelation of gazelle locations at a 5-km scale, NDVI was relevant to discriminate between gazelle presence and absence areas (Table 2). The coefficients for both NDVI predictors, the first- and second-order polynomial, were highly significant (the first being positive and the second negative; Table 2). Variation in biomass between surveys (median of absolute NDVI at each survey), season (spring vs. autumn surveys) and interaction terms did not significantly improve the model and were removed based on the AIC. The model that included vegetation productivity and spatial autocorrelation as predictors explained 25% of the overall deviance (Table 2, model A). This model also classified 76% of both presence and absence blocks, correctly assuming 0·5 probability thresholds.

We employed a model using solely NDVI as a predictor excluding the autoregressive term to predict gazelle habitats independent of any ancillary knowledge on gazelle occurrences (Table 2, model B). While the overall fit of the model decreased, both estimates of coefficients of the NDVI predictors remained significant (Table 2, model B). The reduced model was still very efficient in classifying the gazelle presence data and the omission error did not increase; 77% of gazelle presence blocks were correctly classified (246 of 319); 4% (13) of the presence blocks had, according to the model, too high productivity; and 19% (60) had too low productivity (Fig. 2). However, the commission error increased and, with 48% accuracy (152 of 319), the model was not effective in classifying gazelle absence. Thresholds indicating a probability of gazelle occurrence = 0·5 for this model were at 0·31 and 0·74 of the range of the minimum–maximum scaled NDVI values (Fig. 2).

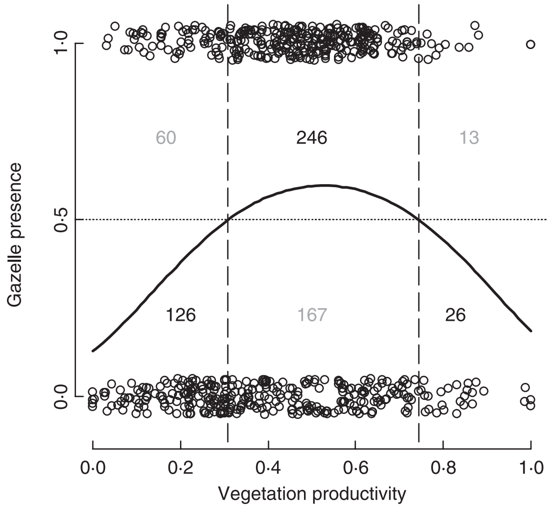

Fig. 2. Probability of gazelle presence predicted based on relative vegetation productivity. Solid line, logistic model; dashed vertical lines, 0·5 probability thresholds for gazelle presence; jittered dots, sample values; black numbers, correctly classified samples based on thresholds; grey numbers, misclassifications.

We used these thresholds to delineate gazelle habitats in the four NDVI data sets of the survey periods. While the average NDVI between surveys varied considerably, with lowest biomass in autumn 2001 and most productivity in autumn 2002, in each survey about 50–65% of the study area was delineated as gazelle habitat (Fig. 3). Consistently across seasons, most areas were predicted to be unoccupied by gazelles because vegetation productivity was too low rather than too high (Fig. 3). We found a pronounced spatiotemporal heterogeneity of NDVI and therefore gazelle habitats between surveys. Only 7% of the study area was never classified as gazelle habitat, and only 15% had a probability of gazelle occurrence above 0·5 across all four seasons (compared with 11% overlap to be expected at a total random distribution, and 49% with maximum overlap). Merely 1% of the study area was located within protected areas and gazelle habitat throughout all four surveys. The average overlap of habitats between seasons (46%) was similar to the average overlap within seasons (43%).

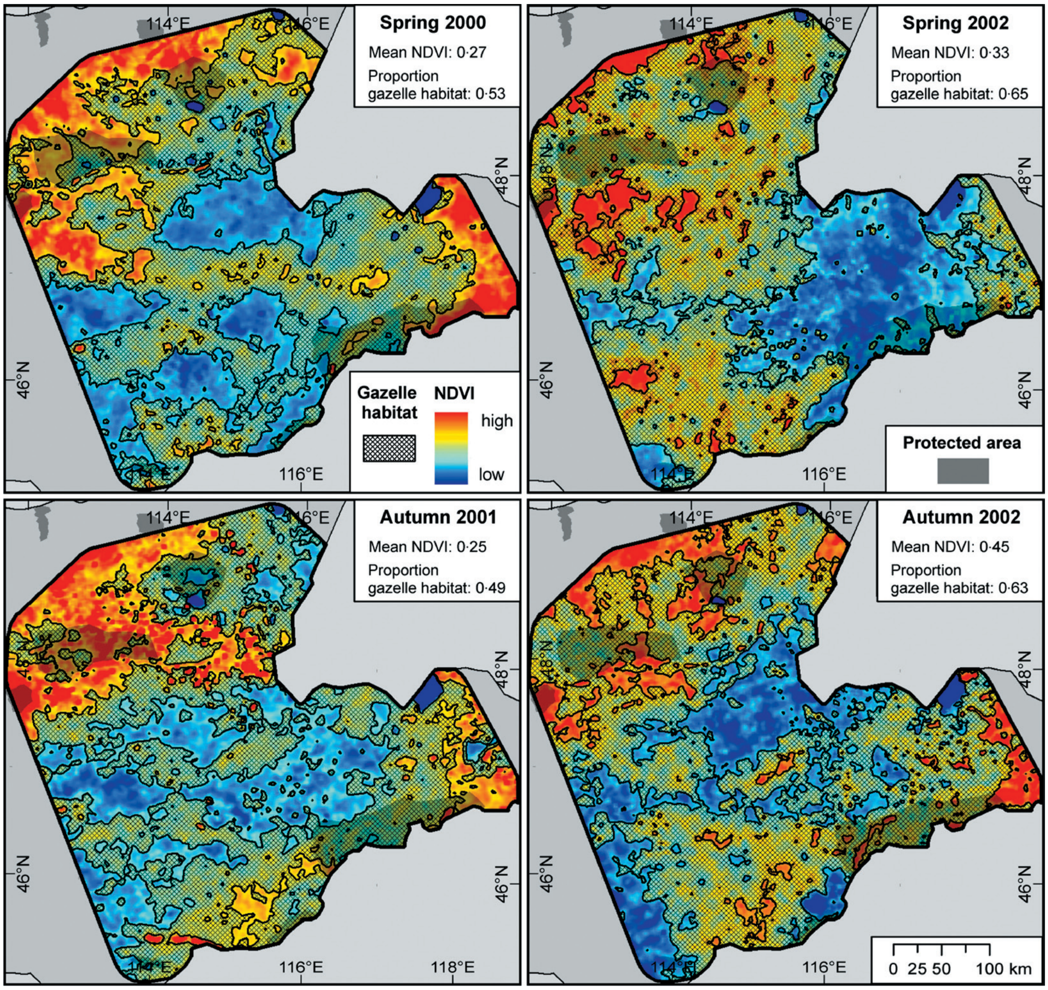

Fig. 3. Distribution of vegetation productivity and gazelle habitat in the study area at four survey seasons. Note the high degree of spatiotemporal habitat variability, specifically in the central part of the eastern steppes.

We tested the predictive power of the model further using gazelle telemetry locations and NDVI data from a 16-day period in July 2001. Random shifts of these locations across a prediction surface calculated from the NDVI had, in only five out of 1000 ($P = 0{\cdot}005$) permutations, a higher average than the average of the actual gazelle locations. The area these gazelles used throughout the entire year comprised a minimum convex polygon of about 45 000 km^2 (Fig. 4, telemetry area). For the second half of July 2001, the model predicted that 56% (≈26 000 km^2) of the telemetry area was preferred gazelle habitat, and 85% of all groups were found within the predicted area (Fig. 4). The remaining 10 gazelle groups were located in low-productivity areas, but always in close proximity to predicted habitat (maximum distance = 7 km; Fig. 4).

Discussion

GAZELLE HABITAT SELECTION AND NDVI

We assessed habitat selection of Mongolian gazelle with regard to vegetation productivity and found a significant relationship between NDVI and gazelle occurrence. Omission errors for both models (with and without spatial autocorrelation) were generally low, and few gazelle-presence locations (24 and 23%, respectively) occurred outside the predicted areas. Consistently, 85% of gazelle relocations from the telemetry study were found within the predicted range. Gazelles preferred an intermediate range of NDVI values independent of variation in total biomass between surveys or survey season.

While areas with low vegetation productivity may simply not offer sufficient forage quantity, resources in high-productivity areas are expected to be limited by altered plant stoichiometry (changes in C : N : P ratios) and an overall decrease in forage quality (Moe *et al.* 2005). As grasses mature, they accumulate structural tissues and their fibre content increases, reducing their digestibility (McNaughton 1984, 1985). Previous studies have related vegetation nutritional content, vegetation quantity and growth state with the foraging ecology of different herbivores (Murray & Brown 1993; Wilmshurst *et al.* 1999; Murray & Illius 2000). Additionally, satellite-based biomass estimates may not only capture quantity, but also indirectly measure vegetation quality. Kawamura *et al.* (2005a) established

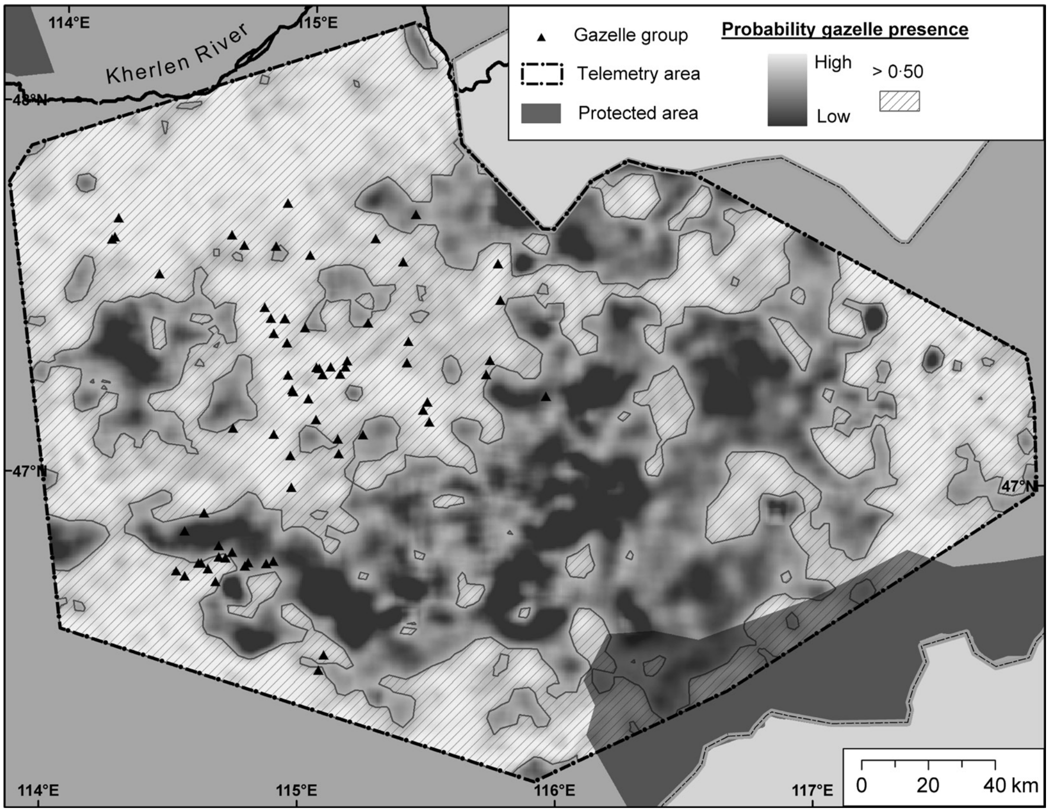

Fig. 4. Gazelle groups relocated in the second half of July 2001 in relation to a prediction surface and habitat thresholds generated from the NDVI-based logistic model. The telemetry area indicates the minimum convex polygon of relocations over the entire telemetry study.

a negative relationship between relative protein content and the Enhanced Vegetation Index for Inner Mongolia, an area close to our study site. Previous studies relating gazelle presence with NDVI were based on less extensive data on gazelle distributions and focused solely on forage quantity in explaining gazelle occurrence (Leimgruber *et al.* 2001; Ito *et al.* 2005, 2006). The present study demonstrates that consideration of forage quality–quantity trade-offs may be important for broad-scale satellite-based habitat models for wild ungulates in temperate grasslands. We suggest that future investigations as to how satellite estimates of vegetation may be related to plant stoichiometry might be worthwhile. In that respect, it would specifically be interesting to compare our method with the approach of Boone, Thirgood & Hopcraft (2006). They calculated the difference of two NDVI scenes and focused on new vegetation growth as one habitat-quality measure for wildebeest in the Serengeti.

NDVI alone, however, was not useful in discriminating gazelle absence. Many areas that were classified as suitable for gazelles had none, a result of excluding spatial autocorrelation in the model. For a constantly moving species, it may simply be that not all suitable habitat is used at any one moment. False negatives are a critical problem in predicting mobile species habitats (Tyre *et al.* 2003). Longer-term or repeated observations may be necessary to gain higher confidence about gazelle absence, but they would be logistically difficult to conduct. Additionally, not only elimination of false negatives, but covariates other than vegetation productivity may be instrumental in refining the current model. Three additional factors that potentially influence gazelle habitat selection are particularly worth considering. First, variation in plant species composition may go along with differences in nutritional quality (Hooper & Vitousek 1998; Reich *et al.* 2001) while productivity rates are similar. Information about species composition and their spatiotemporal dynamics may thus aid efforts to predict gazelle presence. Second, anthropogenic influences, despite the area's sparse human population, may be important, and spatial variation in density of herders may be an informative covariate. Finally, insect harassment has been shown to significantly affect caribou (*Rangifer tarandus*: Walsh *et al.* 1992; Toupin, Huot & Manseau 1996; Weladji, Holand & Almøy 2003). Mosquitoes and biting flies are temporarily abundant at high densities in parts of the eastern steppes. Detailed data on any of these covariates were not available to apply to the gazelle survey data used in this study, and would require additional extensive and repeated field surveys. Obtaining these data would be particularly important to disentangle which of these covariates may be confounded with NDVI (the degree to which species composition, insect density and/or human density are interrelated with NDVI). We also know little about habitat selection throughout winter; nutritional quality of forage in winter generally decreases and the physiology of the rumen in Mongolian gazelles adapts by shifting towards a grazer-orientated digestive strategy (Jiang *et al.* 2002a, 2002b, 2003b). Consequently, gazelle habitat selection potentially could switch towards a preference for higher-biomass areas in winter.

HABITAT VARIABILITY

Throughout the four surveys, we observed a high degree of spatiotemporal heterogeneity of gazelle habitat. While in each season 50–65% of the area was classified as gazelle habitat, the total overlap was only 15%. This is very close to what would be expected if habitats had no temporal or spatial autocorrelation, and would be randomly distributed (11%) and relatively far from the minimum variation at total overlap (49%). Heterogeneity seems to be specifically prominent in the central part of our study area (Fig. 3). These shifts in resource availability not only demonstrate the species' area needs, which are dynamic and may shift between years; it also may illustrate why movement of gazelles appears so irregular and nomadic. Under a regular and seasonal migration regime, we would have expected that the habitat overlap within seasons and between years would be greater than the habitat overlap between seasons. This was not the case, as the average between-season overlap was slightly higher (46%) compared with the within-season overlap (43%). Habitat heterogeneity may be the critical factor explaining far-ranging and irregular movement behaviour enlarging Mongolian gazelles' area needs, as has been demonstrated previously for Thompson gazelles (*Gazella thomsoni*: Fryxell *et al.* 2005).

Yet, little is known about the mechanisms that drive the spatiotemporal variability in plant communities and/or quantity that we detected based on NDVI–satellite imagery. There is, however, evidence for pronounced variation in plant phenology and reversible, non-equilibrium dynamics of plant communities (Briske, Fuhlendorf & Smeins 2003, 2005) when measured on a temporal scale. Comparison of climatic patterns with date of onset of green-up suggests that climatic variation may be a major factor driving changes and interannual variation in plant phenology (Lee *et al.* 2002, Inner Mongolia). Fernandez-Gimenez & Allen-Diaz (1999) demonstrated for a steppe area in central Mongolia that variation in biomass, species cover and functional group cover (forb vs. grass) were all dependent on both grazing intensity and climatic variability. Identifying the degree to which grazing intensities of Mongolian gazelles are sufficient to allow them to shape their own habitat (Hobbs & Swift 1988), as do livestock in Mongolia (Fernandez-Gimenez & Allen-Diaz 1999; Kawamura *et al.* 2005a) or wild ungulates in other grasslands (McNaughton 1985, Serengeti; Murray & Illius 2000), is critical to understanding the grazing ecology of the eastern steppes.

CONSERVATION IMPLICATIONS AND FUTURE APPLICATIONS

Long-distance movement behaviour of grassland ungulates such as Mongolian gazelles increases their vulnerability to habitat loss and fragmentation (Murray & Illius 1996; Berger 2004). Ungulates often need to move across large areas to follow shifts in resource availability (Sinclair 1983; McNaughton 1985; Fryxell, Greever & Sinclair 1988; Murray 1995). Existing protected-area systems usually cover only a fraction of these areas (e.g. wildebeest, McNaughton 1985; Sinclair & Arcese 1995; Thirgood *et al.* 2004; pronghorn *Antilocapra americana*, Berger 2004; caribou, Nellemann & Cameron 1998; saiga *Saiga tatarica*, Bekenov, Grackhev & Milner-Gulland 1998; chiru *Pantholops hodgsoni*, Schaller 1998a), leaving these species exposed to increasing threats of development and poaching.

Mongolian gazelles and their habitat are under increasing threats from intense hunting, transportation infrastructure development, and oil-extraction activities (Pentilla 1994; Reading *et al.* 1998; Asian Development Bank 2002). In 1995, Mongolia's Ministry of Nature and Environment established a series of protected areas and nature reserves to conserve Mongolian gazelles, covering ≈18 800 km^2, but this represents less than 5% of the gazelle's estimated 475 000-km^2 range (Finch 1996). In this study we show that, throughout four surveys, only 1% of the study area was consistently classified as gazelle habitat and located within protected areas. The ranges of Mongolian gazelle are simply too large and variable to be completely included within a single protected area, and excluding humans from these ranges is not only unrealistic, but would have a negative effect on traditional pastoralist societies. The long-term conservation of Mongolian gazelles requires the development of landscape-level conservation strategies for the region (Leimgruber *et al.* 2001; Zahler *et al.* 2004). Landscape-level approaches are required that facilitate traditional rangeland use, retain intact grasslands, and simultaneously promote protection of migrating wild ungulates (Coppolillo 2000). The impacts of deviating from policies promoting open rangelands can be observed in many places. Examples are the changing land-use patterns in the Kenyan side of the Serengeti–Mara ecosystem, resulting in declines in wildlife populations (Serneels & Lambin 2001); the construction of irrigation canals and intensive sedentary livestock grazing in Kazakhstan and Kalmykia, resulting in disruption of saiga migrations (Milner-Gulland 1994); and the fencing in Inner Mongolia, China leading to severe land degradation (Williams 1996).

Our approach, using satellite-based estimates of vegetation productivity to predict wildlife habitat requirements, can directly inform such landscape-level strategies. Wherever an integrative and large-scale conservation framework for grassland ungulates is needed, dynamic models based on high temporal-resolution satellite data can predict habitat patterns for critical periods in their life history (e.g. for Mongolian gazelles calving in late June). Interannual variability of these habitats can also be assessed. Predicted habitat use may then be combined with human land-use needs to create a dynamic management framework that defines conservation actions. It would contain measures that are specific in time and space (e.g. hunting restrictions, limits on vehicle access or other disturbance, livestock grazing restrictions, fence removal) and mitigate between conflicting interests of rangeland use and wildlife needs.

Future research applications and needs include ground truthing to corroborate empirically the relationship between NDVI and forage quantity and digestibility, delineating and estimating interannual variability of calving grounds, and the assessment of long-term spatial and temporal patterns in grassland productivity and gazelle habitats in the eastern steppes.

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