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Biological Conservation 102 (2001) 205–212

BIOLOGICAL CONSERVATION

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# Spatial patterns in relative primary productivity and gazelle migration in the Eastern Steppes of Mongolia

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Received 19 May 2000; received in revised form 20 December 2000; accepted 3 January 2001

**Abstract**

The Mongolian gazelle (*Procapra gutturosa*) of the Eastern Steppes of Mongolia shows seasonal migrations to traditional winter and calving grounds with diffuse movements during the intervening periods. We used a normalized difference vegetation index (NDVI), derived from coarse-resolution satellite imagery, to map relative primary productivity of steppes between April 1992 and December 1995. Productivity peaks were variable between years, but winter and calving grounds had highest NDVI scores during periods of use by gazelles. Gazelle movements to these areas track shifts in primary productivity across the steppe. Diffuse movements in summer were not matched to peaks in productivity. Productivity 'hotspots' utilized by gazelles during critical periods in their life cycle should be first priority for conservation and the impact of livestock grazing on these areas should be evaluated.


*Keywords:* Mongolian gazelle; Ungulate migration; Primary productivity; Steppe; NDVI

## 1. Introduction

Zeer, as Mongolian gazelles (*Procapra gutturosa*) are locally known, are the dominant and characteristic feature of one of the last remaining temperate grasslands — the Eastern Steppes of Mongolia. The zeer is especially noted for its annual migrations, during which herds ranging in size from 35,000 to 80,000 animals can be observed (Lhagvasuren and Milner-Gulland, 1997). Migrations of the gazelles do not follow a clear north/south axis, but rather are characterized by herd movements between winter and calving grounds that are scattered throughout the steppes (Lushchekina et al., 1985; Jiang et al., 1998).

Zeer have been described as 'permanent migrants', with only females pausing in their movements during the brief calving season (Lhagvasuren and Milner-Gulland, 1997). Zeer are seasonal breeders with a rutting season that lasts from mid-November to early February and a short birthing season, usually sometime between mid-June and mid-July (Lushchekina, 1990, in Lhagvasuren and Milner-Gulland, 1997). The onset of the calving period is very variable and may depend on climatic conditions during the previous year (Lhagvasuren and Milner-Gulland, 1997). During calving periods, groups of up to 40,000 females can be observed in areas of about 35 km$^2$, during an approximately 2-week period (Lushchekina et al., 1985). Up to 90% of the females in a group may give birth within a period of 4 days (Lushchekina, 1990 in Lhagvasuren and Milner-Gulland, 1997).

Aggregations of zeer also occur during the winter (Lhagvasuren and Milner-Gulland, 1997; Wang et al., 1997; Jiang et al., 1998). These aggregations appear to be driven by a search for snow-free areas. The number of congregated animals appears to fluctuate with the severity of the winter (Lhagvasuren and Milner-Gulland, 1997; Wang et al., 1997).

In recent years, there has been increasing concern about declines in geographic range and population numbers of zeer (Lhagvasuren and Milner-Gulland, 1997; Reading et al., 1998). Until as recently as the 1950s,

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0006-3207/01/$ - see front matter 
PII: S0006-3207(01)00041-6

zeer were commonly found throughout most of Mongolia and adjacent regions belonging to Kazakhstan, the Russian Federation, and China — an area of approximately 1.2 million $km^2$ (Fig. 1). Now, the species is restricted to $< 400,000$ $km^2$ — the eastern portion of the original range (Fig. 1; Lushchenkina et al., 1985; Lhagvasuren and Milner-Gulland, 1997; Reading et al., 1998).

Zeer population numbers also declined in the last half of the 20th century. Zeer were abundant throughout the 1940s with a total population size estimated at 1,000,000 animals (Bannikov, 1954, in Lhagvasuren and Milner-Gulland, 1997). By the 1970s, these numbers had dropped sharply to as few as 170,000–180,000 animals (Lushchekina, 1990, in Lhagvasuren and Milner-Guland, 1997; Tsagaan, 1978, in Lhagvasuren and Milner-Guland, 1997). The population recovered somewhat in the 1980s and 1990s, with population estimates between 300,000 and 400,000 animals for the 1980s (Lushchekina et al., 1985) and at least 400,000 animals in the 1990s (Lhagvasuren and Milner-Gulland, 1997). Based on these estimates the total population has been reduced by half during only 50 years.

Zeer population estimates are admittedly crude and vary widely depending on the source of the estimate. There is good reason to credit more the lower estimates. For example, current estimates range from 400,000 to 2,000,000 animals (Lhagvasuren and Milner-Gulland, 1997). The larger number would mean the population has doubled since the 1940s even as its range collapsed to an area less than 1/3 of its original size. This is very unlikely and most recent publications on Mongolian gazelles assume a severe population decline for the species (Lushchenkina et al., 1985; Lushchekina, 1990 in Lhagvasuren and Milner-Guland, 1997; Lhagvasuren and Milner-Gulland, 1997; Reading et al., 1998).

The declines in both numbers and range appear to be caused by overharvesting, poaching, and the overstocking of livestock (Lhagvasuren and Milner-Gulland, 1997; Jiang et al., 1998; Reading et al., 1998). The selection of optimal protected areas for zeer conservation is challenging because of the lack of basic data on habitat needs. However, areas where animals aggregate (i.e. winter and calving grounds) and corridors between these areas should be of particular importance to the species. We hypothesized that zeer migrations are driven by a search for forage and that calving grounds, especially, should exhibit an abundance of green grasses to support large numbers of female zeer.

To evaluate our hypothesis, we explored the usefulness of satellite imagery and Geographic Information Systems (GIS) for linking seasonal patterns in primary productivity to migratory patterns in gazelles. If such a system works, identification of important areas for gazelle conservation in the vast Eastern Steppes could be significantly aided by satellite imagery, remote sensing and GIS technology.

Satellite imagery and remote sensing technology commonly have been used to assess habitat extent and quality in ungulate studies (e.g. Unsworth et al., 1998; Bowyer et al., 1999; McShea et al., 1999). For rangeland ungulates, aboveground net primary productivity (ANPP) is strongly correlated with habitat quality

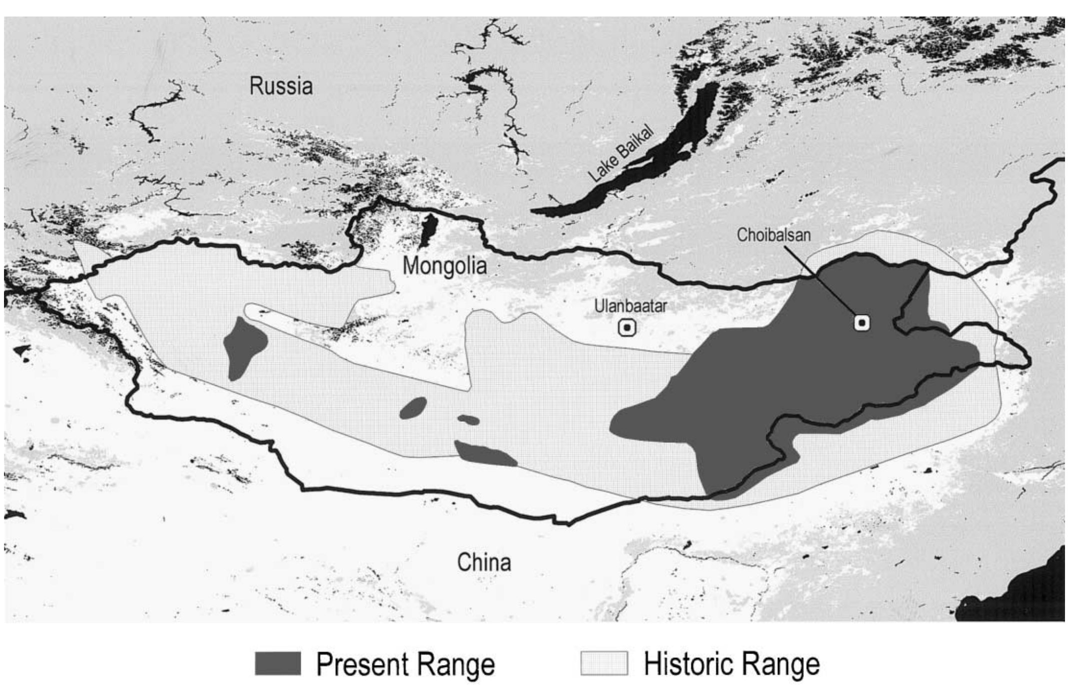


Fig. 1. Historic and present geographic distribution of Mongolian gazelles (*Procapra gutturosa*).

(McNaughton, 1985; Frank and McNaughton, 1992; McNaughton, 1993). It is possible to use the normalized difference vegetation index (NDVI; Lillesand and Kiefer, 1999) calculated from Advanced Very High Resolution Radiometer (AVHRR) satellite imagery as an index for relative ANPP. The NDVI represents the difference in reflection between the near-infrared and the red parts of the electromagnetic spectrum (Eidenshink and Faundeen, 1994) and works well to measure productivity because healthy green vegetation reflects strongly in the near-infrared but absorbs most light in the red. There are good statistical relationships between the NDVI and biomass or ANPP (Cilhar et al., 1991; Paruelo and Laurenroth, 1995; Paruelo et al., 1997), and NDVI has been used to estimate herbivore stocking rates for the rangelands of Argentina (Oesterheld et al., 1998). We used the NDVI derived from AVHRR data to test our hypothesis that zeer migrations are correlated with shifts in primary productivity.

## 2. Methods

Our study focused on the current range of the remaining zeer populations in the Eastern Steppes of Mongolia (Lhagvasuren and Milner-Gulland, 1997).

The NDVI was calculated from AVHRR imagery by using channel 1 (visible, VIS) and channel 2 (near-infrared, NIR) in the equation:

$$\mathrm{NDVI} = \frac{(\mathrm{NIR} - \mathrm{VIS})}{(\mathrm{NIR} + \mathrm{VIS})}$$

NDVI values range between $-1.0$ and $+1.0$. Increasing values $>0.0$ indicate increasing ANPP, while negative values generally represent non-vegetated surfaces such as barren lands, rock, water or ice.

We downloaded NDVI data for eastern Mongolia (upper left corner 51′N; 107′W; lower right corner 41′N; 120′W) from the United States Geological Survey Earth Resource Observation Data Center (EDC) through the Internet (http://edcwww.cr.usgs.gov/landdaac/1KM/1kmhomepage.html). The data were part of the 1-km AVHRR global land data set that has been archived and distributed by the EDC and the European Space Agency (ESA; Eidenshink and Faundeen, 1994). The EDC processed the raw data according to defined and standardized methods including radiometric calibration, atmospheric correction, computation of NDVI, geometric registration and compositing. Details of these processing steps are described by Eidenshink and Faundeen (1994). The product we downloaded was a 16-bit, 10-day composite NDVI image with 1.1-km resolution. Each picture element (pixel) in the composite represented the maximum NDVI value for a defined 10-day period (Eidenshink and Faundeen, 1994).

NDVI images for Mongolia are available for the period from 1 April, 1992 to 30 September, 1993, and 1 February, 1995 to 31 December, 1995. We downloaded all images and, using visual inspection, chose the best image for each month for our analyses. Despite the fact that using 10-composites of AVHRR imagery for the calculation of NDVI significantly reduces cloud contamination of pixels, we could not find acceptable NDVI images with cloud cover $<30\%$ for December 1992.

We delineated three types of habitat within the zeer range (i.e. winter, summer, and calving grounds) using a combination of maps from the literature (Fig. 2; Lushchenkina et al., 1985; Lhagvasuren and Milner-Gulland, 1997) and expert knowledge of staff members of the Eastern Steppes Biodiversity Project (ESBP) funded by the United Nations (UN) Global Environment Facility (GEF). Because calving occurs during a very short time period and at variable dates, and because zeer migrate over very large areas, it is unlikely that all calving grounds are currently known. However, if our analysis demonstrates a close link between primary productivity, measured by satellite sensors, and known seasonal gazelle movements, the technique could be used in the future to predict where unknown calving areas might be located.

All areas known to be used by the gazelles as winter, summer, and calving grounds were entered into a GIS by digitizing the outlines on-screen and using data from the Digital Charts of the World (DCW; ESRI, 1993) as a back-drop. All NDVI images were registered to the coordinate system of the DCW data set using major geographic landmarks that are clearly visible on the satellite image. In the Eastern Steppes these landmarks are large water bodies such as Kherlen Gol, Buir Nuur and Hulun Nuur (Fig. 2).

Monthly averages for NDVI were calculated using all image pixels from all areas of each of the three habitat types, summer, winter and calving grounds. The monthly overall average was calculated using pixels from all habitats combined and represents an index of monthly overall productivity. To get an index of relative biomass production in the different parts of the geographic range, we subtracted the overall average value from each of the monthly average values for the different habitats. We used Wilcoxon signed rank tests (SYSTAT, 1996) to test whether relative differences in NDVI averages between habitats were due to chance alone.

## 3. Results

### 3.1. Seasonal patterns in primary productivity

Monthly averages for NDVI demonstrate strong seasonal patterns in ANPP, with the highest average values between June and September and the lowest average values between November and February (Fig. 3).

However, the date of maximum and minimum NDVI values in these two seasons varied considerably between the years. Differences in average NDVI values between the three different parts of the zeer range are most pronounced in the maximum values of the summer and the minimum values of the winter.

### 3.2. Relative productivity differences between winter and calving grounds

Relative differences in NDVI show a switching pattern in productivity between winter and calving grounds (Fig. 4). During the summer months, the NDVI average

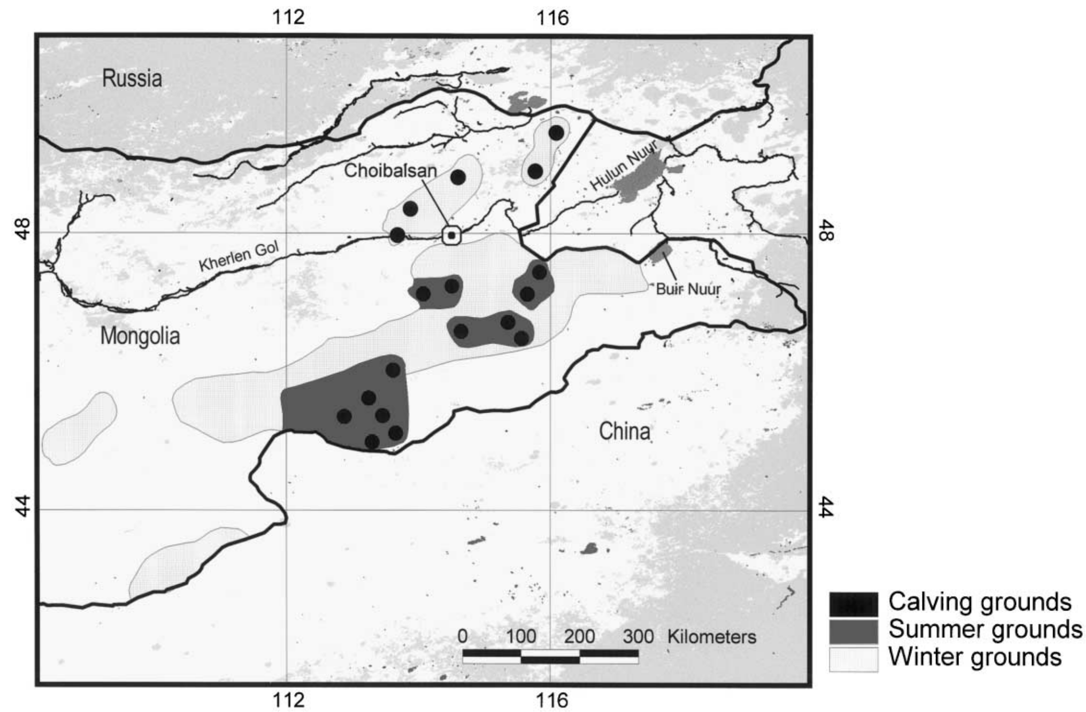


Fig. 2. Extent of known calving, summer, and winter grounds for Mongolian gazelles.

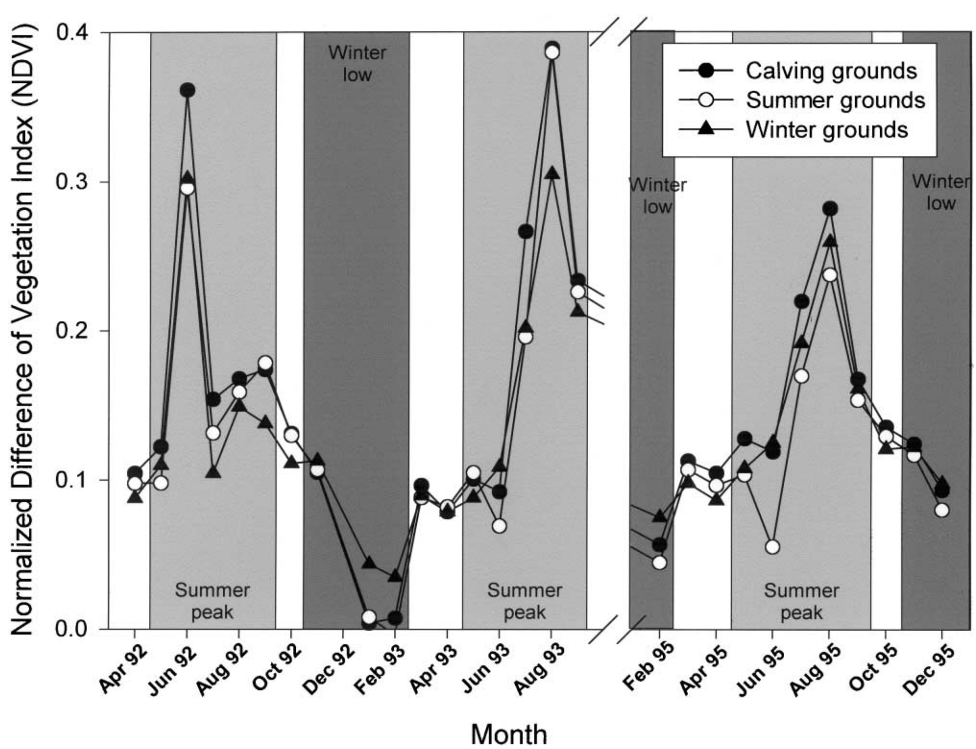


Fig. 3. Seasonal patterns in aboveground net primary productivity (ANPP) approximated by monthly averages for the normalized difference vegetation index (NDVI).

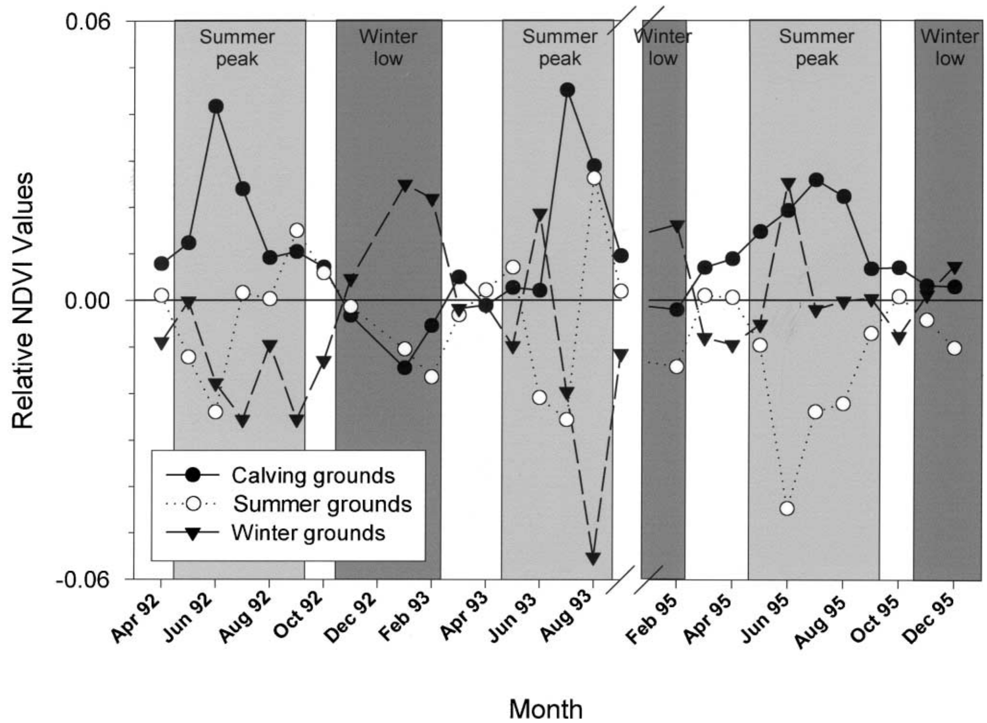


Fig. 4. Relative differences in aboveground net primary productivity (ANPP) between calving, summer and winter grounds. ANPP was approximated using the normalized difference vegetation index (NDVI).

Table 1
Two-sided probabilities for significant differences in relative NDVI in different areas of the Mongolian gazelle's geographic range during seasons of high (May–September) and low (November–February) productivity

| Productivity | | Calving area | Summer area |
|---|---|---|---|
| High | Summer area | 0.002 | |
| | Winter area | 0.002 | 0.955 |
| Low | Summer area | 0.116 | |
| | Winter area | 0.046 | 0.028 |

is relatively highest in the calving grounds, but during the winter months the pattern is reversed with the winter grounds having a relatively higher average NDVI. No clear biomass pattern for the summer grounds is apparent.

To test for differences in NDVI values between calving, summer and winter grounds, we split the year into two periods; a period of overall high productivity (May–September) and a period of overall low productivity (November–December). The results from Wilcoxon signed rank tests demonstrated that the observed patterns of switching of high relative NDVI values in calving and winter grounds with seasons were significant (Table 1). There was a significant difference in relative NDVI between the calving grounds and either summer or winter grounds during periods of high productivity (Table 1). During the same time period, there was no significant difference between the summer and the winter grounds. Similarly, we found a significant difference in relative NDVI between winter grounds and either calving and summer grounds during periods of low productivity, but there was no significant difference between calving and summer grounds.

## 4. Discussion

Our results clearly demonstrate that zeer follow green pasture during crucial parts of their life cycle; parturition and wintering. When localized high population densities occur, due to females giving birth or cold weather conditions, animals congregate in areas of high relative plant productivity. This is particularly evident during calving periods, when the concentrated activities of female zeer coincided with the occurrence of plant productivity 'hotspots', as measured by the NDVI.

Birth synchrony has been attributed to two ultimate causes; a short growing period and effective predators (Rutberg, 1987). For ungulates, early lactation is when nutritional requirements of mothers and predation risks of fawns reach their maximum (Bowyer et al., 1998a, 1999). Selection of calving grounds should reflect the tradeoffs between these processes (Berger, 1991, Bowyer et al., 1999). In the first scenario — a short growing season — young must reach a minimum body size prior to the onset of winter and timing of parturition is usually constrained by the gestation period. While these factors can result in birth synchrony, they do not require that individuals congregate prior to parturition.

In the second scenario — effective predators as a major source of mortality for young — females can 'swamp' predators by producing young over a short time span in a constrained area (Estes and Estes, 1979). Although predator swamping has been rejected as a possible explanation for birth synchrony in moose (*Alces alces*, Bowyer et al., 1998b) and bighorn sheep (*Ovis canadensis*, Rachlow and Bowyer, 1991), this behavioral response may occur in barren-ground caribou (*Rangifer tarandus*, Bergerud and Page, 1987) and wildebeests (*Connochaetes taurinus*, Estes and Estes, 1979). Zeer movements to calving grounds are similar to the movements of open-steppe ungulates, such as caribou and wildebeest, with zeer selecting the most productive habitat available to them during the birthing season. Without field studies, it is difficult to know if the congregation of females in areas of high productivity reduces risk of predation to fawns, or if the movements primarily give access to abundant and nutritious forage needed for lactation.

Our study demonstrates that currently known calving grounds are productivity 'hotspots'. However, there may be more productivity 'hotspots' in the steppes that are not utilized by gazelles during calving season. If there were many available patches for the gazelles to choose from, then congregation would not result from females simultaneously accessing patches for abundant food. Other factors, including predator swamping, might account for this kind of selection. Detailed mapping of habitat selection by zeer and of primary productivity are needed to exclude this possibility. The latter needs to be accomplished using mid-resolution satellite data that is collected at high frequency, such as the newly available MODIS images. Similarly, because our study evaluates the relative differences in NDVI between different areas in the steppes, we cannot evaluate the magnitude of the difference in actual ANPP. Detailed studies that combine frequent seasonal field measurements of ANPP across different steppe habitats with spectral information from satellite imagery are needed to get estimates for actual ANPP. These data are currently not available but will be essential for future monitoring of the steppe and its zeer populations.

In winter, when overall plant productivity is low, zeer are found across larger areas, which exhibit seasonally higher ANPP than either the summer or birth areas. The trend for herbivore movements to track plant productivity was not evident during other times of the year, such as the summer. Once birthing season ended, the overall higher productivity of the region (Fig. 3) negates the necessity of tracking 'hotspots'.

It is not surprising that animal movements track shifts in plant productivity, as this result has been reported for other grassland systems (McNaughton, 1985, Pearson et al., 1995). Tracking plant phenology has also been reported for ungulates making seasonal altitudinal migrations, such as red deer (*Cervus elaphus*) in the Swiss National Park (Schloeth and Burckhardt, 1961) and the Bavarian Alps, wapiti (*Cervus elaphus*) in the alpine regions of Canada (Morgantini and Hudson,1989) and black-tailed deer (*Odocoileus hemionus*) in the Cascade Mountains of California (Smith, 1989).

Using relatively coarse and inexpensive technology such as AVHRR data, we were able to track productivity changes in the Eastern Steppes and relate them to zeer movements. AVHRR images have a resolution (i.e. 1 $km^2$) which cannot be used to detect subtle habitat differences, but works well to examine coarse-grained patterns of habitat quality and ungulate habitat selection. The coarse-grained nature of habitat selection by zeer is similar to selection of wintering habitat by ungulates in Yellowstone National Park (Pearson et al., 1995). Fires in previous years at Yellowstone created broad differences in productivity across the Park that were reflected in the winter movements of bison (*Bison bison*) and elk *(Cervus elaphus*). We would expect the movements of other open-steppe ungulates, such as caribou and saiga to show the same coarse pattern.

The coarse-grained differences in productivity across the Eastern Steppes of Mongolia are probably due to fire history, and differences in soil composition and landscape contour (Shantz, 1954; Frank and McNaughton, 1992, Pearson et al., 1995). The ability of previous researchers and current Mongolian wildlife staff to identify traditional calving and winter grounds indicates that differences in productivity across the steppe are relatively consistent. The potential ANPP at a site is constrained by soil and landscape features, but there are annual differences in ANPP tied to fluctuations in precipitation (Lauenroth and Sala, 1992). These annual differences in magnitude and timing were evident in our examination of the NDVI, but the calving grounds maintained their status as grounds with relatively high NDVI between the months of May through September. An examination of small mammal distributions across the Chinese portion of the Eastern Steppe showed macro-patterns of plant productivity were better indicators of small mammal biodiversity than micro-patterns of productivity (Wang et al., 2000). Over the range of annual precipitation observed in this study, the macro-pattern of productivity was a good measure of zeer movements.

Although we used known calving and winter grounds to complete this analysis, the life history and movements of these gazelles are, in general, poorly known (Lushchekina et al., 1985, Jiang et al., 1998). The use of an NDVI index derived from AVHRR data could locate potential calving and winter grounds in regions that are not as well studied, or in regions where gazelle populations have been extirpated (Jiang et al., 1998). Other migratory steppe animals in Mongolia that are either endangered (see Reading et al., 1998), or included in plans for reintroduction (i.e. takhi, *Equus przewalskii*), may also benefit from an analysis of their landscape to locate and protect productivity 'hotspots'.

Gazelles share most of the Eastern Steppes with livestock. Although there is no direct correlation between livestock grazing and ANPP (Milchunas and Lauenroth, 1993), there is little doubt that natural grazers influence grasslands differently from agricultural grazers (McNaughton, 1993). The loss of zeer in China is speculated to be as much a result of overgrazing as overhunting (Wang et al., 1997). High plant productivity areas are often the focus of both livestock (Oesterhold et al., 1998) and native ungulate (McNaughton, 1985) activity. Livestock consumption of the annual productivity within the calving grounds in early spring may bring the productivity of these areas below levels capable of sustaining herds of female zeer. Whether zeer are capable of shifting calving grounds to meet shifts in productivity is unknown. If they are not capable of shifting, or if no other suitable areas are available, overgrazing of calving grounds would have severe consequences on zeer conservation.

During the 20th century, the conversion of the Mongolian economy to a Soviet central market system, and the continuing transition from a nomadic to a more sedentary culture, have coincided with the decline of gazelle numbers. The Mongolian government has recently set aside over 1/3 of the country's lands for protection. With the large migration movements reported for zeer and other steppe animals such as tahki, Asiatic wild ass *(Equus hemionus*), goitered gazelles (*Gazella subgutturosa*), and bactrian camels (*Camelus bactrianus*), this scale of protection may be warranted, if these animals are to be conserved. Our results suggest that calving areas for Mongolian gazelles should have priority for protection, followed by extensive areas of the winter range.

## Acknowledgements

We thank the UN-GEF Eastern Steppes Biodiversity Project (ESBP) and all its staff for supporting the work and providing valuable insights into the ecology of the Mongolian gazelles and eastern steppes. All analyses were performed at the Conservation and Research Center's Spatial Analysis Lab and we are grateful to John Rappole for letting us use the facility and Melissa Rodden for providing technical support. We also thank Tom Small and Melissa Songer for their help during data collection, analysis and preparation of the manuscript and Kate Christen for review of the final manuscripts. Funding was provided by the National Zoological Park's Sisely Grant and the GEF-ESBP. Last but not least, we want to acknowledge ESRI and ERDAS for providing generous GIS and image processing software donations to the Smithsonian Institution's Conservation and Research Center.

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