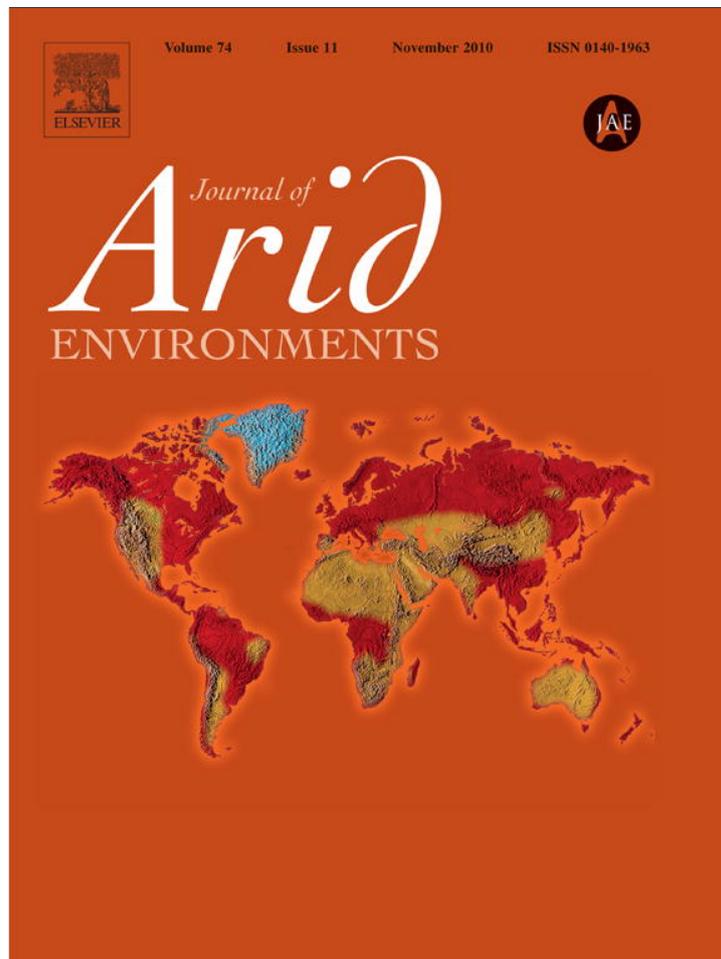


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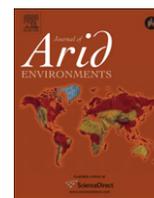
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Annual movements of Mongolian gazelles: Nomads in the Eastern Steppe

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ABSTRACT

Determining the scale and pattern of, and the influences on, the movements of Mongolian gazelles is important because their numbers and range have been reduced significantly, and their remaining grassland habitat faces further fragmentation and degradation. Therefore, during 2000–2005 we monitored movements of individually marked Mongolian gazelle calves and adult females in the Eastern Steppe of Mongolia to identify variation in seasonal range sizes and locations, group sizes, and range characteristics. Annual range size for calves varied over an order of magnitude (800–18 700 km²), and none of 9 calves tracked for a full year returned to their birth site. Adult gazelles ranged widely (14 000–32 000 km² annually) and individuals captured together showed little range overlap. Seasonal shifts in range use suggested gazelles are readily able to take advantage of changing conditions, but the lack of consistent use of seasonal ranges is characteristic of a nomadic movement strategy. Developing strategies that protect ungulate populations that demonstrate nomadic movements is an important consideration in future conservation decisions. Understanding the ecology driving these movements will be an important next step.

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1. Introduction

Human activity increasingly threatens wide-ranging ungulate populations (Berger, 2004; Harris et al., 2009). Conservation of these unique movements is challenging because, at its simplest, it often means placing vast areas of human-occupied habitat under protection, and thus in conflict (e.g., Thirgood et al., 2004). Though some ungulate movement behaviors and the factors that affect them are fairly easily identified, others are complex and will likely require creative conservation solutions to ensure their existence into the future (Berger, 2004; Homewood et al., 2001; Wilcove and Wikelski, 2008). To date, such solutions have not been forthcoming and rapid collapse has been the well-documented consequence of partially

protected and poorly understood populations (Bolger et al., 2008; Harris et al., 2009).

Mongolian gazelles, *Procapra gutturosa*, are one of the few remaining abundant, wide-ranging grassland ungulates, and their habitat is one of the largest remaining intact grazing systems in the world (Schaller, 1998). Enduring decades of intense hunting, the Mongolian gazelle population declined significantly and prompted its listing as regionally endangered (Clark et al., 2006). The Eastern Steppe of Mongolia, the species' last stronghold, represents a fraction of what was once a 1.5 million-km² temperate grazing ecosystem (Tong et al., 2004). This remaining grassland habitat faces further fragmentation and degradation from oil exploitation, and road and railroad development, that continue to threaten to the species' survival (Gunin et al., 1999; Humphrey and Sneath, 1999).

Mongolian gazelles are believed to exhibit a variety of movement patterns, ranging from sedentary, to distinctly migratory, to permanently nomadic (Heptner et al., 1961; Lhagvasuren and Milner-Gulland, 1997; Mueller and Fagan, 2008). Gazelle

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movements between supposed or potential seasonal ranges are restricted by fences adjacent to railways to deter livestock or along political boundaries to deter humans (Ito et al., 2005; Lhagvasuren and Milner-Gulland, 1997; Wang et al., 1997).

Conservation efforts thus far operate on the premise that Mongolian gazelles' movements follow a traditional migratory concept where on an annual basis gazelle herds migrate in large groups to known seasonal pastures using established movement corridors in predictable time frames (e.g., Leimgruber et al., 2001). As such, some protected areas have been established to preserve what was observed to be the most important habitat, but without full understanding of what the criteria were for quality habitats (Lhagvasuren and Milner-Gulland, 1997). These protected areas and reserves were later found not to be consistently suitable and indeed were only used by gazelles for a fraction of the year (Mueller et al., 2008). Additionally, less than 2% of steppe habitat in Mongolia is under official protected status and there is much debate as to whether fixed protected areas are an appropriate conservation strategy (Mueller et al., 2008; Reading et al., 2006). As a result, the current protected area strategy might not be an effective means of protecting the Mongolian gazelle population. Meanwhile economic development activities that threaten the integrity of the steppes continue unabated in the absence of a sound conservation plan for this ecosystem.

Determining the scale and pattern of, and the influences on, the movements of Mongolian gazelles is clearly an important step in creating successful strategies for their long-term conservation and management. Thus, we captured and fit newborn calves with expandable VHF radio collars, and adult female gazelles with Argos platform terminal transmitting (PTT) collars, and monitored their movements during 2000–2003 (for calf survival analyses, see Olson et al., 2005a). By doing so, we sought to identify the predictability of the seasonal and annual distribution of individuals, as well as their associations with each other.

2. Materials and methods

2.1. Study area

This study focused on Mongolian gazelles that occupy the 275 000-km² region of eastern Mongolia that is the largest, least fragmented and most ecologically intact portion of the Eastern Steppe (Appendix 1 electronic version only). In this area, Mongolian gazelles exist at densities ranging between 3 and 11 gazelles/km² and the population is estimated at slightly over 1.1 million (Olson, 2008).

Elevation ranges from 565 to 1777 m asl, but there is no distinct elevation gradient. Annual precipitation across the steppe averages 228 ± 67 mm ranging from 100 mm along the ecotone between steppe and desert steppe to 400 mm along the steppe forest-steppe ecotone bordering the Khingan and Khenti Mountain ranges (www.weatherunderground.com; Yu et al., 2004a,b). Grasses (*Stipa* spp., *Cleistogenes squarrosa*, *Leymus chinensis*) dominate, with forbs (*Allium* spp.), dwarf shrubs (*Artemisia frigida*), and shrubs (*Caragana* spp.) fairly common (Olson et al., in press). Steppe woodlands are rare but do occur as elm (*Ulmus* spp.) patches in dry washes, willow (*Salix* spp.) stands, and Siberian apricot (*Armeniaca sibirica*) scrub (Gunin et al., 1999).

Approximately 60% of the region's 200 000 human inhabitants live in small village settings or are herders grazing sheep, goats, horses, cows, and camels (National Statistical Office – Mongolia, 2004). Natural resource extraction (minerals, coal, and oil) and industrial-scale hay harvesting is intensifying (Olson et al., 2009;

Reading et al., 2006). Mongolia's land tenure system generally consists of state ownership of pastureland with grazing rights determined via historic land occupation. Local pasture use is allocated by local government officials, and winter shelters can be placed under long-term lease (Fernandez-Gimenez, 2006). Aside from human hunting pressure (Olson, 2008), Mongolian gazelles are prey for wolves (*Canis lupus*) and eagles (*Aquila* spp.) (Olson et al., 2005a).

2.2. Movement patterns

In 2003, vehicles and drive nets were used to capture adult female gazelles in early autumn. During the morning and evening hours gazelle groups were located from a distance, and 15- and 20-m length nets were erected in a double row approximately 75 m long. Vehicles (usually 3–5) were used to haze gazelles into the net. Once entangled, gazelles would be restrained by tying their hind and front legs together with cotton rope, and a stretchable wrap was placed over their eyes (Ito et al., 2005, 2006). Adult gazelles were fit with Argos PTT collars (Harris et al., 1990) programmed to transmit locations once per day. Protocols for capturing and marking gazelles were approved by the University of Massachusetts at Amherst Institutional Animal Care and Use Committee.

When animal movement data were processed, all 1, 2, and 3 location classes were retained in addition to class A and B locations deemed accurate for mammals that have wide ranging movements (as recommended in the Douglas filter algorithm; Ver. 6.4, <http://alaska.usgs.gov/science/biology/spatial/manual.html>). Relocation data were plotted and distances between successfully obtained locations were calculated.

For adult Mongolian gazelles, the annual and seasonal range use was calculated from minimum convex polygons (MCP) of point locations from the respective season of interest. Seasonal ranges were determined using locations obtained during seasons roughly corresponding to major differences in rainfall, snow cover, temperatures and behaviors (e.g., summer = 1 Jul–21 Sep; autumn = 22 Sep–20 Dec; winter = 21 Dec–21 Mar; spring = 22 Mar–20 Jun; calving = 21 June–1 July; Olson et al., 2005a). To identify any association and fidelity to specific regions we calculated a simple index of overlap for the seasonal MCP's of the three adult gazelles captured at the same location and time (e.g., Fieberg and Kochanny, 2005) where the area of overlap between two ranges is divided by the total area of an individual's range. This was done for individual range overlap as well as a single overlap index for all three animals. Also, three of the transmitters provided data beyond a single year and we compared overlap of inter-annual seasonal ranges of those, as well.

In 2000, 2001, and 2002, we captured newborn Mongolian gazelles by hand in two main regions north and south of the Kherlen River, fit them with expandable VHF collars and recorded their behavior (Odonkhuu et al., 2009) and movements (details of capture methods can be found in Olson et al., 2005a). In any one year, all calves were collared in the same general region, but not always within the same calving aggregation. When a radio-marked calf was subsequently located, map coordinates were recorded and, when possible, an estimate of the herd size was made; when necessary, locations were estimated by triangulation of compass bearings. Calves collared in 2000 were monitored for 6 months after capture, calves collared in 2001 and 2002 were monitored for a full year (Olson et al., 2005a).

Sizes of groups with radio-marked calves were calculated by season and year. A Kruskal-Wallis test for equality of median group sizes was conducted to assess seasonal differences in group size. The frequency with which calves that were marked together were subsequently located together was also calculated.

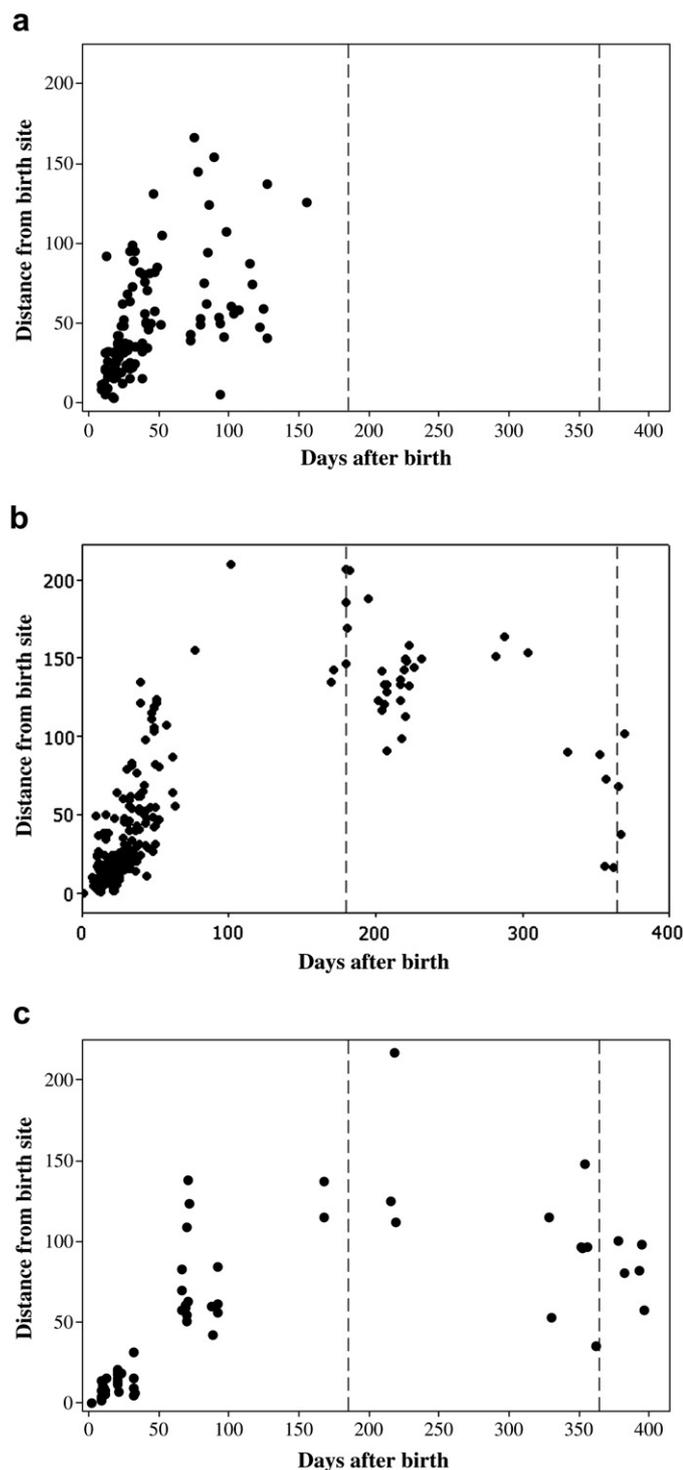


Fig. 1. Distances traveled from birth sites by radio marked gazelle calves. Dashed lines represent the breeding season (day 185 – late December) and the following year's calving period (day 365 – late June). a. 2000 (South of Kherlen River). b. 2001 (South of Kherlen River). c. 2002 (North of Kherlen River).

3. Results

3.1. Movements of calves

In 2000, Mongolian gazelle calves ($n = 10$) captured in the same or nearby locations did not move together and spread out over a large area (Appendix 2 in electronic version only). After 85 days

calves had each traveled 42–154 km ($\bar{x} = 99 \pm 47$ km, $n = 7$) from their birth site (Fig. 2). Individual range use (MCP) up to 155 days for the 2000 cohort varied from 1 327–6 249 km² ($\bar{x} = 3843 \pm 1967$ km²; $\bar{x} = 6.0 + 3.0$ locations each, range = 3–10), and the total area (MCP) used by all of the marked calves during the 155 days was 32 080 km².

In 2001, calves ($n = 41$) captured in the same general location (and similar to those monitored in 2000), also did not move in a synchronized fashion (Appendix 3 in electronic version only). After about 185 days (January) calves had each traveled 134–206 km ($\bar{x} = 172 \pm 29$ km, $n = 8$) from their birth site (Fig. 1), and the greatest distance between simultaneous locations of two marked calves was 260 km. For calves monitored for an entire 12-month period (July 2001–June 2002), individual range areas (MCP) varied from 861 to 18 711 km² ($\bar{x} = 6168 \pm 5943$ km², $n = 9$; $\bar{x} = 7.3 + 3.2$ locations each, range = 4–14). During the entire 12-month period, the area encompassing (MCP) all marked calf locations measured 45 514 km². Calves monitored throughout the year ($n = 9$) generally moved east from their birth site and summer range to autumn, winter, and spring range (Appendix 3 in electronic version only). By the next calving season, calves did move back west but did not show any obvious fidelity to their specific birth sites.

In 2002, calves that were captured north of the Kherlen River ($n = 20$) were also furthest from their birth site (i.e., ~210 km) in about late January (Fig. 1; Appendix 4 in electronic version only). Calves relocated after 1 full year were between 35 and 148 km from their birth site ($\bar{x} = 95 \pm 49$, $n = 5$), and the total annual range covered by these 5 calves was 24 824 km². The calves monitored in 2002 in the northern regions shifted further north for the winter months and returned in a southerly direction, but also did not return to their exact birth site.

3.2. Group sizes and associations of calves

In 2000, median group size of marked calves was somewhat higher during the summer (700) than in the autumn (348; $H = 2.87$, $P = 0.09$, $df = 1$) (Table 1). In 2001, group sizes were similar in summer (640) and autumn (710), but apparently were largest in winter (1600), and smallest in spring (420; $H = 6.77$, $P = 0.08$, $df = 3$). There were no statistical differences (seasonal group sizes which ranged from 155 to 1200; $H = 4.53$, $P = 0.21$, $df = 3$) in 2002. In 2001, after an initial 7-day period when calf locations were not recorded, two or more marked calves were located in the same herd on 26 different occasions, or 14% of opportunities (of 182 total relocations) for any 2 of the 58 calves to be together.

3.3. Movements of adult females

In September 2003, 11 adult female gazelles were captured in two different locations; of these, 4 were successfully monitored for

Table 1
Size of groups in which radio-marked gazelles calves were observed in the Eastern Steppe of Mongolia.

Year	Season	Mean ± SD	Median	Range	N
2000	Summer	1576 ± 2215	700	2–10 000	90
	Fall	2313 ± 2878	348	38–3500	20
2001	Summer	1296 ± 2158	640	2–18 000	156
	Fall	820 ± 436	710	450–1300	3
	Winter	3570 ± 5547	1600	300–20 000	14
2002	Spring	468 ± 411	420	31–1000	4
	Summer	938 ± 1136	450	3–4100	28
	Fall	231 ± 185	155	68–450	5
	Winter	975 ± 955	975	300–650	2
	Spring	5630 ± 10338	1200	70–31 000	9

Table 2
Seasonal range sizes (km²; Minimum Convex Polygons) for adult female gazelles captured and radio collared in September 2003, and located almost daily via Argos satellite technology, at locations southeast and north of the Kerlen River. Sample sizes for each season's MCP are presented in parenthesis (ss).

Location	ID no.	Autumn	Winter	Spring	Calving	Summer	Annual
Southeast	26335	7 009 (62)	3 295 (80)	13 316 (65)	374 (10)	240 ^a (15)	32 298
	41599	17 195 (83)	2 395 (75)	5 955 (58)	363 (6)	3 063 (31)	30 840
	41608	8 725 (62)	3 285 (74)	3 868 (60)	362 (6)	12 820 (40)	28 155
North	41602	8 455 (79)	4 709 (79)	2 022 (46)	104 (8)	3 457 (32)	14 661

^a Transmitter ceased to function shortly after the summer season.

at least the next 4 of 5 seasons. Three of these were captured south of the Kherlen River in the southeastern portion of the steppe, and 1 was captured 25-km north of the Kherlen River (Appendix 5 in electronic version only). The other 7 transmitters either never transmitted usable location data or failed to transmit within a few months after capture and were not used in this analysis.

The annual range sizes varied more than 2-fold (range = 14 661–32 298 km²; \bar{x} = 26 489 km²), with the smallest range occupied by the gazelle captured north of the Kerlen River (Table 1). Seasonal ranges also varied 2 to 4-fold among individuals, with winter ranges usually smaller than autumn and spring ranges (Table 2); females did not remain at distinct locations during the 10-day calving season (range = 104–374 km²).

Seasonal range overlap was greatest in autumn (overall average = 0.44) when animals were captured together, but thereafter overlap was generally low (winter and spring) or non-existent (calving and summer) (Table 3, Fig. 2). By calving season, one female (26335) was 230 and 237 km distant from the other two (41599 and 41608) who were 27 km apart but whose MCPs for calving did not overlap.

There was no inter-annual seasonal range overlap for Gazelle 41608 between the first and the second autumn or winter range (Fig. 3). Inter-annual seasonal range overlap for Gazelle 41599 was also low, with the first autumn range overlapping the second autumn range by 14%, and by winter there was no inter-annual seasonal range overlap (Fig. 3).

4. Discussion

4.1. Movement patterns

In general, movement patterns of ungulates can be categorized with respect to the predictability and spatial pattern of movements over the course of seasons and years (Mueller and Fagan, 2008). Sedentary ungulates (i.e., range-residents) reside in relatively small yearly ranges, generally excluding movements among areas at distances greater than the maximum daily movement of a species. Resident ranges are not temporally static: animals' use of such areas can vary seasonally as a function of available resources. However, within populations of range resident species, individuals show dispersed spatial distributions when compared to populations of migratory or nomadic species.

Table 3
Mean seasonal range (MCP) overlap (%) for three adult female gazelle captured and marked at the same time (Sep 2003) and location (south of the Kerlen River).

Pair ID nos.	Mean (Individual overlap values)				
	Autumn	Winter	Spring	Calving	Summer
41608/41599	56 (38/74)	13 (11/14)	64(48/80)	0 (0/0)	0 (0/0)
41608/26335	37 (33/41)	17 (17/17)	7 (3/10)	0 (0/0)	–
41599/26335	38 (22/54)	4 (3/4)	11 (7/15)	0 (0/0)	–
Mean	44	11	27	0	0

Migratory ungulates have regular seasonal and round-trip movements to and from spatially disjunct seasonal ranges, with relatively little time spent on movement between areas (Berger, 2004; Nicolson et al., 2002; Pennycuik, 1975). Migration occurs in a diverse number of taxa (Benhamou and Bovet, 1989; Biegler, 2000; Gardner and Gustafson, 2004) and is observed in systems with regular, seasonal fluctuations in resource availability (Pennycuik, 1975). Well-known ungulate migrations include those of caribou (*Rangifer tarandus*) in North America (Gardner and Gustafson, 2004) and wildebeest (*Connochaetes taurinus*) in Africa's Serengeti (Morales and Ellner, 2002). The boundary between movement strategies that yield either range residency or migration is often distinct.

Nomadic behavior occurs when resources fluctuate irregularly on a multi-year time frame over large areas; as a result, animal distribution patterns can vary widely among years. Nomadism may be a good descriptor of such patterns, but the term suffers from a variety of definitions (Belovsky, 1984; Conradt et al., 2003; Gray and Kennedy, 1994; Murray, 1995; Nicolson et al., 2002). Nomadic movements lack the inter-year predictability that characterizes range residency and migration, and are instead characterized by unpredictable paths varying among individuals for any given year or among years for any given individual. Nomadism is comparatively little understood, although elements of unpredictability are a common movement feature of many ungulates.

To date, the most complete ecological hypothesis of the year-round movements of Mongolian gazelles was put forth by Heptner et al. (1961) in which a complex series of movements were thought to be dependent on the spatiotemporal distribution of grasslands with different grass:forb ratios, snow depth, and primary productivity. It was believed that, in summer, gazelles move in search of quality *Stipa* dominated grasslands and seek winter range with a greater abundance of forbs where snow is less able to form a crust making access to forage easier. Mueller et al. (2008) developed a habitat model using satellite-based vegetation indices to identify habitats that Mongolian gazelles are more likely to be found in and demonstrated that there is a high degree of spatial and temporal variation in the distribution of this preferred habitat throughout the steppe. The importance of the ability to access quality habitat during periods when these suitable habitat patches are highly restricted was pointed out by Olson et al. (2009) after observations of huge aggregations of gazelles during a severe drought.

Our data show that gazelles in the eastern and northern regions of the steppe move over great distances, tend to shift seasonal ranges, but do not have strong fidelity to any particular calving region. These indicators suggest that the movements of Mongolian gazelles are best described by nomadism. Importantly, adult females monitored for more than a single year did not utilize the same areas used in the previous year or years and quickly moved into different ranges than animals they were previously in the same group with. The inconsistent use of winter range by our gazelle calves in 2001 and the only partial return to calving regions by the 2001 cohort in 2002 offers additional evidence that gazelles do not have consistent migratory pathways and calving grounds are not

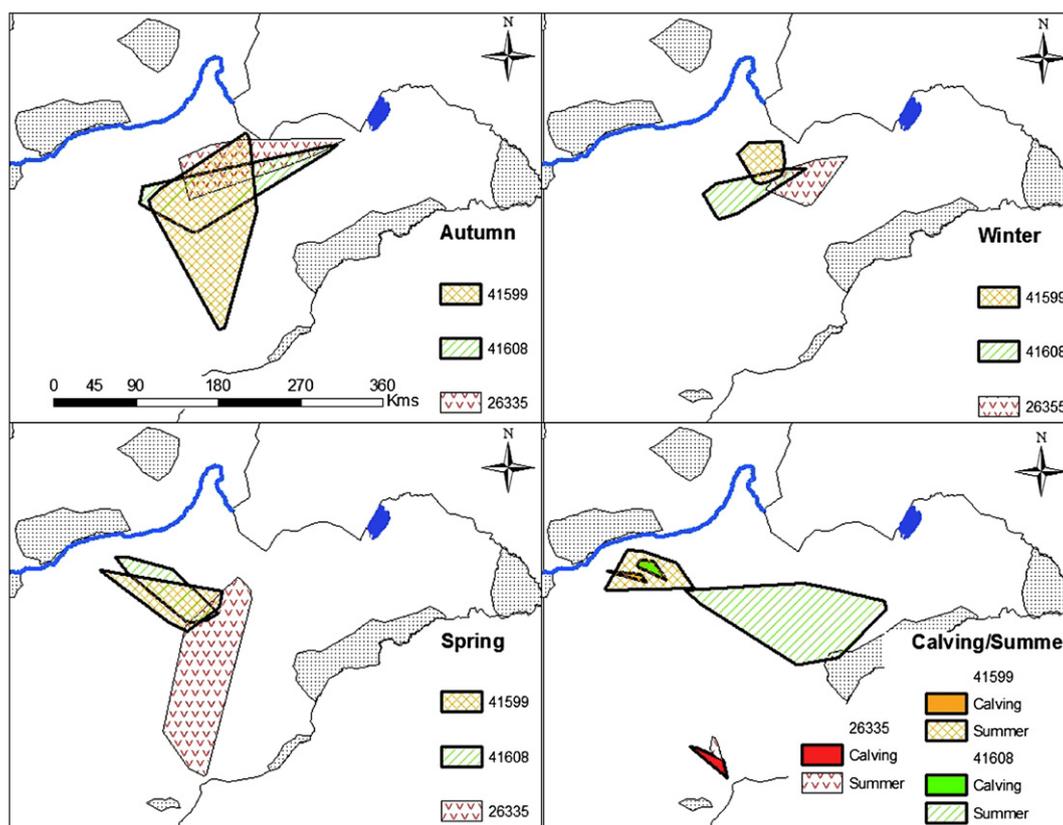


Fig. 2. Seasonal range overlap of 3 adult female Mongolian gazelle captured at the same location in 2003 in southeastern Mongolia. Protected areas (stippled, non-convex polygons) also indicated.

consistently returned to, although these calves would not have been mature animals. The shift north during winter demonstrated by calves marked in 2002 and the movements east by calves in 2000 and 2001 suggest that suitable winter range conditions exist in a variety of regions throughout the steppe. Genetic differences between regions should be expected if Mongolian gazelles followed a fixed migratory pathway with traditional breeding and calving areas. The Mongolian gazelles, however, have high nucleotide diversity (Sorokin et al., 2005), further evidence that Mongolian gazelles are highly flexible in adopting nomadic long distance movements with respect to their life history strategy to cope with highly variable, non-equilibrium grassland ecosystem dynamics (Carmicheal et al., 2007).

4.2. Sociality and factors influencing movements

Median group size of radio-collared calves was an order of magnitude larger than median group sizes observed during surveys by Olson et al. (2005b); median group size ranged between 14 and 42) and Olson (2008); median group size 10–12 in 3 regions). Our larger observed group sizes may reflect their invariable inclusion of calves, or behavioral attempts by gazelles to find relief from biting insects in summer and, in winter, from eagles and wolves through dilution by two groups of the population that stand the most to lose (Walsh et al., 1992). The poor fidelity to birthing sites shown by calves may either reflect a change in vegetation productivity from year to year making the site less attractive (Mueller et al., 2008), the presence of biting insects during the lying out phase, or high incidence of calf mortality experienced by mothers the previous year (Wiseman et al., 2006).

Our results suggest that gazelles often utilize different ranges between summer and winter, and recent advances in understanding the ecological drivers for these movements have been made. Ito et al. (2006) found inconsistent differences in summer NDVI (Normalized Difference Vegetation Index) values when comparing seasonal ranges in 2 study areas and suggested that NDVI values alone cannot explain the seasonal movements of gazelles. Mueller et al. (2008) found that Mongolian gazelles are tracking changes in vegetation productivity but do not seek the areas of highest productivity. One hypothesis that needs testing is the possibility that the presence of mosquitoes and biting flies may be excluding gazelles from occupying this habitat. The addition of insect harassment as an ecological driver of movements would expand the list of Harris et al. (2009), who summarize five ecological drivers of large-scale ungulate migrations (grasslands quality/quantity, vegetation green-up, surface water, snow depth and traditional areas), but do not include insects.

The steppe is a relatively homogenous ecosystem; apart from lightly rolling hills there is minimal elevation change. Water sources are not overly abundant, but are scattered throughout the steppe. Snow melt in the steppes does not appear to occur at an elevation or directional gradient. Also, there is no evidence of regionally distinct concentrations of minerals important to females and calves during late pregnancy and calving that would lead to the development of consistent round trip migrations between ranges (Olson, 2008). There may be nutritional hotspots scattered throughout the steppe that are utilized when forage, insect, snow, and human disturbance conditions are all satisfactory to Mongolian gazelles in order for them to occupy these areas. An absence of distinct differences in abiotic characteristics that seem to be prominent for other ungulate species that exhibit round trip

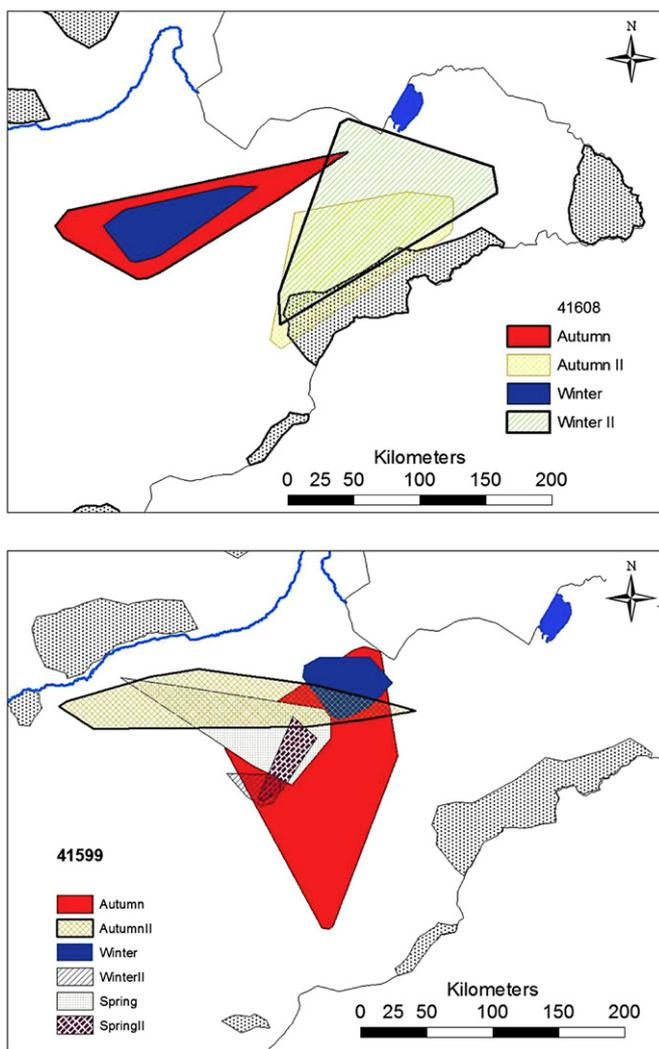


Fig. 3. Inter-annual and seasonal range overlap of 2 adult female Mongolian gazelles monitored for 2 years. Protected areas (stippled, non-convex polygons) also indicated.

migrations is an important feature that allows the variability of quality forage, as well as the interaction with biting insects and the conditions they need for their existence, to lead to nomadic movements in Mongolian gazelle. It may be that, at times, conditions do exist such that round trip annual movements are observed. This would help explain why Mongolian gazelle calves did appear to 'return' from a winter range to calving areas.

4.3. Comparison with other ungulates

Pronghorn (*Antilocapra americana*) populations found in the Greater Yellowstone Ecosystem exhibit flexibility in their migratory strategy, with up to 30% of the members in one population remaining on winter range each year while others followed a highly predictable migratory pathway (Berger, 2004; White et al., 2007). Fires and grazing pressure changing winter range quality were reasons for flexibility in this system. The Jackson Hole elk (*Cervus elaphus*) herd displays flexibility between range residency, migratory and nomadic behaviors (Boyce, 1991). There, migration (distances up to 100-km) follows an elevational gradient where snowfall and green-up are the cues to migrate. In another population of pronghorn in South Dakota, calves born in habitat with greater patchiness of winter forage dispersed twice as far as calves

born in less patchy winter forage (Jacques and Jenks, 2007). Moose (*Alces alces*) in Sweden migrated when snow quality deteriorated to a point where movement of calves was difficult (Ball et al., 2001).

The annual migration cycle of North American caribou is characterized by high fidelity to calving grounds in the northern parts of their annual ranges. Although there are traditional areas of winter use, these can vary between years. The term 'migration' typically implies fidelity to each discrete seasonal areas and regular round-trip movement between these areas (Berger, 2004; Thirgood et al., 2004), but post-calving caribou movements in the six months from their calving season habitat (Jun 1–15) to their winter habitat (Dec 1–Mar 31) do not utilize any obvious corridors and appear more haphazard than the regularity implied by 'seasonal migration'. This is in clear contrast to their spring migration movements, which take place at a predictable time (Apr 1–May 31), utilize similar corridor routes year after year, and (unlike Mongolian gazelles) end up on the same calving grounds.

In Africa's Serengeti ecosystem, wildebeest migration is linked to nutritional demand by lactating females and changes in primary productivity at other times of the year operating within a complex relationship of facilitation between species resulting in a clockwise annual movement spending the dry season (winter equivalent) in the NW corner where dry season rainfall is slightly more than other regions (Bell, 1971; Boone et al., 2006; Murray, 1995; Musiega et al., 2006). It is the dry season survival rates that had the highest variability which was closely tied to the amount of rain received in the dry season (Mduma et al., 1999). Importantly, and particularly related to movements of Mongolian gazelles, Fryxell et al. (2005) demonstrated that Thomson's gazelles (*Gazella thomsoni*) in the Serengeti follow stochastic rainfall events and thus take advantage of ephemeral food sources.

5. Conservation implications and future directions

The ability of species to incorporate flexible movement strategies to better adapt to environmental variation may vanish as human-induced changes to habitat increases. If current barriers continue to be maintained or the steppe is developed to a degree that accessibility of the mosaic of suitable habitats is restricted or major parts no longer exists, gazelle population numbers could drop dramatically over a short period of time (Bolger et al., 2008).

Mongolian gazelles are sensitive to human occupation of the grasslands (Olson, 2008) yet their absence or very low densities in such areas may still reflect a reduction in alternative sites to go to and cause gazelles forced to remain in disturbed sites to suffer from reduced survival and lowered reproductive success (Gill et al., 2001). Conservation and management efforts would benefit from efforts that aim to identify areas throughout the steppe that are free of human activity and place more strict occupancy (grazing or extractive activities) regulations on them which would create a mosaic of steppe where habitat would be available for gazelles. It is essential that grassland management policies must maintain the integrity of traditional pastoral strategies as it is critical for the health of Mongolia's non-equilibrium grassland ecosystems and the populations of Mongolian gazelle that survive within (Ellis and Swift, 1988; Fernandez-Gimenez and Allen-Diaz, 1999; Fernandez-Gimenez, 2006). As demonstrated by Ito et al. (2006), movements of Mongolian gazelles can be easily disrupted by a single structure (in that case, a fence).

The observed shift in seasonal range use demonstrates that there is either a shift in habitat quality or a switch in nutritional requirements that trigger Mongolian gazelle to move in search of important habitat. The type of winter habitat required for gazelles, and its distribution within the grasslands, has not been investigated. As postulated by Heptner et al. (1961), it may be possible that

winter range is defined by areas that have a higher proportion of forbs so that foliage is less likely to be matted down during heavy snow conditions. In addition to easier access, forbs tend to have greater nutritional values and would help maintenance of body condition in winter. To understand what is influencing the movement of gazelles off of winter ranges, several questions need to be pursued; 1) Are gazelles being driven from better habitat by biting insects and flies while at the same time having their range constricted by an increasing livestock population? 2) Is the timing of emergence of these insects the cue to move out of winter range into areas where these insects are absent and moving back onto summer range when conditions reverse?

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Appendix Supplementary material

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.jaridenv.2010.05.022.

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