

A Literature Review of Mongolian Gazelle (*Procapra gutturosa*) Ecology from 1998 to Present

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Abstract

With respect to Mongolian gazelles a great deal of new knowledge has been gained over the past 10-12 years since the last species reviews were conducted. Advances in molecular techniques have helped to clarify the status of the genus *Procapra* and the relationship between the three extant species within and have highlighted the high genetic heterozygosity throughout the population. New morphological studies have focused on dimorphism between the sexes and the evolutionary development and role the enlarged larynx seen in males. Mongolian gazelles have long been the subject of intense debate with respect to their role as reservoirs for pathogens such as Foot and Mouth Disease virus, but with long term collection of serum from adults and calves it has been shown that gazelles are passive recipients of a virus harbored and spread by other means. Great strides have been made in the study of Mongolian gazelle forage ecology and their overlap in diet with domestic livestock as well as better understanding the physical adaptations needed for survival in a harsh environment with long periods of low quality forage availability by switching to browsing and grazing strategies. Using satellite tracking and remote sensing technology gazelle movement patterns are much better understood. Movements are more nomadic in nature and linked to tracking changes in quality habitat in time and space and less dictated by what was previously thought to be traditional migratory patterns. Mongolian gazelle have highly synchronized calving events which coincide with the start of the summer solstice and calf weights are correlated with the previous winter's harshness. Calves demonstrate behavior associated with 'hider' species for the first few weeks of life before they begin to aggregate in large herds and move to different grazing grounds. Advances in survey methodologies have led to a better assessment of the population status of Mongolian gazelles and the most recent published studies estimated there to be 1.126 million gazelles living within Mongolia's border. Density varies widely and is negatively correlated with the presence of households. Future studies should focus on research that helps us better evaluate population dynamics, forage preference, behavioral interactions, and the role gazelles play in ecosystem function.

Key words: landscape species, Mongolian gazelle, *Procapra*, species research review, temperate grassland

Introduction

Periodic assessments of the scientific understanding of a species ecology and status are important for assessing conservation strategies and to re-prioritize future research directions. Taxon specific research increases our capacity to develop targeted management and conservation planning and helps minimize conflict between human development interests and the focal species ecological needs. Advances in wildlife research capabilities such as new techniques to analyze genetic material to using satellites to

monitor movements of individuals and advances in remote sensing technology have greatly improved our knowledge of Mongolian gazelle ecology and an updated literature review is due.

Since Heptner *et al.* (1961) published the first assessment of Mongolian gazelle (*Procapra gutturosa*) ecology and distribution, there have been three comprehensive reviews of the scientific literature and the species conservation status (i.e., Sokolov & Lushchekina, 1997; Lhagvasuren & Milner-Gulland, 1997; Jiang *et al.*, 1998). However since these publications a great deal of effort was dedicated to improving

the scientific understanding of Mongolian gazelles and their ecology. These advances will allow conservation practitioners and agencies charged with their management to better address an increasing number of threats. The goal of this work is to summarize the wide range of recent research conducted on Mongolian gazelle in order to set a new benchmark in our understanding of the species ecology.

Phylogenetics

Molecular evidence now supports the placement of three extant species in the genus *Procapra*: *P. gutturosa*, the Mongolian gazelle; *Procapra picticaudata*, the Goa or Tibetan gazelle; and *P. przewalskii*, the Przewalskii's gazelle (Groves, 2000; Kuznetsova & Kholodova, 2003). The status of *P. przewalskii* as a separate species or a subspecies of Tibetan gazelle was questioned by Rebholz and Harley (1999). Using mitochondrial RNA gene sequences, Runhua *et al.* (2003) determined that *Procapra przewalskii* was more closely related to *Procapra gutturosa* and deserved its current species status, *Procapra przewalskii*, and that the genus *Procapra* is, indeed, monophyletic.

Nucleotide diversity in Mongolian gazelles is exceptionally high (similar diversity as in kob, *Kobus kob*, and Grant's gazelle, *Gazella granti*, two other highly mobile species) at $5.85 \pm 2.92\%$ (Sorokin *et al.*, 2005). Using estimated mutation rates of ungulates of 10-20% per million years, Sorokin *et al.*, (2005) reported that Mongolian gazelles emerged in their current location 200,000-400,000 years before present. Paleontological records place the emergence of Mongolian gazelles sometime during the upper Pleistocene (Heptner *et al.*, 1961). Between 150,000 and 300,000 years before present during a period of mountain glaciation, Mongolian gazelles existed as two distinct breeding populations and after which mixed as one larger population (Sorokin *et al.*, 2005). Throughout the Mongolian gazelles' geographical range there are few differences in the mitochondrial DNA suggesting that throughout their range Mongolian gazelles exist as a single panmictic population (Sorokin *et al.*, 2005; Kholodova *et al.*, 2002).

Morphology

Mongolian gazelles are sexually dimorphic; adult males have a larger body size and have

horns as well as having a large highly developed larynx (Sokolov & Lushchekina, 1997). At birth calves weigh slightly larger than females (4.17 ± 0.51 vs. 3.97 ± 0.54 kg) and weights are directly correlated with the previous winter's average temperature (Olson *et al.*, 2005b).

The evolutionary enlargement of the male larynx is unique among all bovids by having a paired lateral laryngeal ventricle (Frey & Riede, 2003; Frey & Gebler, 2003). This enlarged larynx is retracted to as much as 30% of its resting vocal tract length during the display of head up barking behavior used to round up females during rut (Frey *et al.*, 2008a). During the rut, the male larynx is highlighted by the growth of elongated dark guard hairs along the ventral side of the lower neck (Frey *et al.*, 2008a; Frey *et al.*, 2008b). The deep guttural bellows produced are used to advertise condition to breeding females and competing males. The handicap endured from the larynx swinging loosely during locomotion likely is outweighed by the profits gained in attracting mates and thus increasing their reproductive success (Frey *et al.*, 2008).

Immunology

Mongolian gazelles are known to experience mass mortality events from diseases such as Foot and Mouth Disease, *Pasteurella* spp., and hoof rot (caused by the bacterium, *Fusobacterium necroforum*) (Lhagvasuren & Milner-Gulland, 1997). Identification of the cause of such mass die offs proved difficult as carcasses were often in remote areas and the pathology difficult to assess after many weeks.

Mongolian gazelles are vulnerable to infections during exceptionally wet summer rainy seasons. During late summer of 1998 when, after a month of above average rainfall, foot rot infected a large proportion of the population, with yearlings affected the greatest (Schaller & Lhagvasuren, 1998). The hooves of infected animals become soft, allowing infection to enter, and the resulting swelling makes moving difficult and animals either starve or die of toxemia due to the infection.

In a review of the helminth fauna of ungulate species of Mongolia, a total of 12 species of helminthes were documented to occur in Mongolian gazelles with a new species

of helminth (*Paradictyocaulus gutturosa*) described by Danzhan & Ganbold (1999; cited in Sharhuu & Sharkhuu, 2004). Three *Sarcocystis* species (Sporozoa: Coccidia: Sarcocystidae) were found in localized connective tissue of Mongolian gazelle (Odening *et al.*, 1996). Lux *et al.* (1997) described a new species of chewing louse (Phthiraptera: *Tricholipeurus zaganseeri*) from Mongolian gazelle. Fecal samples from Mongolian gazelles collected in autumn 1999 were infected with 4 types of parasites: *Strongyles* like species, *Nematodirus* spp., *Skrjabinema ovis*, and *Avitellina* spp. (Deem *et al.*, 2001).

Mongolian gazelles have high antibody prevalence to numerous viral agents, particularly parainfluenza-3 and bovine respiratory syncytial virus, both of which cause respiratory disease in livestock, but there is an unknown pathogenic response in Mongolian gazelles (Deem *et al.*, 2001). Mongolian gazelles also had positive antibody titers to infectious bovine rhinotracheitis, a common herpesvirus known to infect a variety of non-domestic ungulates, bovine viral diarrhoea/mucosal disease, sheep/goat poxvirus, *Leptospirosis* serovars, and foot and mouth disease virus (Deem *et al.*, 2001).

The epidemiology of foot and mouth disease in Mongolia and the role Mongolian gazelles have in its persistence is not well developed, yet is the subject of controversial management debates (i.e. culling large numbers of gazelles in outbreak areas to construction of fences to prevent gazelles from entering certain regions). Outbreaks of foot and mouth disease were reported in the Eastern Steppe in 2000, 2002, and 2004 [a 2010 outbreak was confirmed in the Eastern Steppe, Nyamsuren Pers. Comm.]. Mongolian gazelles tested in 1998 and 1999 were not seropositive to foot and mouth disease, but tested positive (67% prevalence) in a 2003 study (Nyamsuren *et al.*, 2006). This suggests that Mongolian gazelles are passive recipients of the disease; however, it is not clear if they can become carriers; or if it is necessary for the disease to remain persistent in domestic livestock (Nyamsuren *et al.*, 2006).

Forage Ecology

Mongolian gazelles shift their feeding habits seasonally in response to differences in food

quality available to them and are classified as intermediate feeders (Jiang *et al.*, 2002b). This feeding strategy allows Mongolian gazelles to take advantage of the widest range of forage available in a habitat with a high degree of spatial and temporal variation in its vegetation condition and species distribution (Junsheng *et al.*, 1999; Jiang *et al.*, 2002b). Mongolian gazelles respond to these changes by increasing the size of the parotid gland and the surface area of rumen during the non-growing season when forage is at its driest and poorest condition (Jiang *et al.*, 2003).

Heptner *et al.* (1961) postulated that Mongolian gazelles seek quality grass-dominated pasture during the growing season, while moving into habitats that have a higher proportion of forbs during the non-growing seasons, especially during winters with high amounts of snowfall, as forbs are better at preventing snow from compacting vegetation. In the Hulun Buir grassland of China, crude protein concentrations are 18–29% in spring, but fall to 2.5–5.6% outside of the growing season (Jiang *et al.*, 2002a). Mongolian gazelles in the Hulun Buir selected a higher proportion of forbs during the spring, but graminoids dominated their diets in other seasons (Junsheng *et al.*, 1999). This forage selection by Mongolian gazelles contradicts the hypothesis put forth by Heptner *et al.*, (1961) that Mongolian gazelles move into areas that have a higher amount of forbs due to them being more accessible in deep snow. However, the study conducted by Jiang *et al.* (2002a) was in an area where the presence of a greater proportion of grasses may have affected gazelle forage selection. However, in the steppes and desert steppe habitats of Mongolia, gazelles eat a higher proportion of forbs, lending partial support of the hypothesis by Heptner *et al.* (1961) that gazelles seek areas with greater forbs during the winter when resources are most restricted (Yoshihara *et al.*, 2008; Schaller, 1998).

Mongolian gazelles overlap in food habits with domestic sheep and goats and, although they do not graze on the same pasture simultaneously, the potential remains for forage competition as human and livestock density increases (Campos-Arceiz *et al.*, 2004 Yoshihara *et al.*, 2008). It was estimated that Mongolian gazelles can consume up to 86 kg/ha per year of biomass from the steppe compared to a horse

which can consume as much as 200 kg/ha per year (Abaturov *et al.*, 2008).

Movements

Much attention has focused on understanding the movement patterns of Mongolian gazelles. Long believed to be migrants following fixed routes at predictable time periods, research shows this to be only a partial picture of a more complex relationship between nutritional demands of Mongolian gazelle and the constantly fluctuating state of the nutritional qualities and availability of the habitat they are seeking. The Normalized Difference Vegetation Index (NDVI) facilitated progress in this field (Pettorelli *et al.*, 2005). Based on historical records of calving and wintering locations (Lhagvasuren & Milner-Gulland, 1997; Lushchekina *et al.*, 1985 [in Leimgruber *et al.*, 2001]), it was reported that gazelles are likely tracking changes in primary productivity during the growing season, seeking out snow-free areas in winter with the selection of calving grounds based on the emergence of productivity 'hotspots' within the steppes (Leimgruber *et al.*, 2001).

More recently, adult female gazelles fitted with ARGOS transmitters were found to have large annual range sizes (up to 32,000 km²) with little overlap between seasons and years (Olson *et al.*, 2010). After their first year of life, individually marked calves did not return to their birth site; this suggests that calving grounds are not traditional but rather vary from year to year as forage conditions change (Olson *et al.*, 2010). Annual movements of adult gazelle are on the same scale as North American caribou (*Rangifer tarandus*) but demonstrate a more chaotic and unpredictable pattern more resembling movements best described as nomadic (Mueller & Fagan, 2008; Mueller *et al.*, in press).

The railway and adjacent barbed-wire fencing that links Ulaanbaatar with Beijing, China was believed to be a significant barrier to movements of gazelles between seasonal pastures (Sokolov & Lushchekina, 1997). By tracking adult gazelle fitted with ARGOS satellite collars, Ito *et al.* (2005) was able to document the barrier effect of the fencing built along the Ulaanbaatar to Beijing railway. After comparing NDVI values along an

east-west gradient perpendicular to the railway it was determined that Mongolian gazelles are being prevented from passing to better quality pasture further east during the winter; thus being constrained to surviving the winter in a region with lower quality forage available could lead to reduced survival of gazelles in this region (Ito *et al.*, 2005). Gazelles were also monitored in the south and middle Gobi regions that are characterized by a western migration to winter ranges occurred (Ito *et al.*, 2006), similar to descriptions by Heptner *et al.*, (1961). As documented along the railway, Mongolian gazelles were found to be tracking changes in primary productivity; however, winter range use often did not occur in areas that had greater biomass availability (Ito *et al.*, 2005). Thus, the spatial and temporal patterns in vegetation productivity alone, as revealed from analysis of the NDVI, do not seem to fully explain gazelle habitat selection.

Mongolian gazelles show a preference for grasslands in the intermediate ranges of vegetation productivity (approximated by NDVI), at least during the non-winter seasons (Mueller *et al.*, 2008). It is likely that the highest regions of vegetation productivity require too great an energy cost to seek out and that Mongolian gazelles are taking an energy maximizing approach and accepting the trade off of foraging in habitat with higher biomass but lower nutritional value and higher fiber. In habitats where the vegetation is experiencing a high rate of growth may also be infested with mosquitoes and biting flies due to recent rainfall and the presence of standing water, or perhaps are areas occupied by livestock and people and the vegetation is continuously cropped prompting a high rate of regeneration (Mueller *et al.*, 2008).

The relationship between vegetation productivity and the importance of access to quality habitat was highlighted during the summer of 2007 when a severe drought restricted suitable habitat available to Mongolian gazelles, resulting in the largest concentration of gazelles documented to date (Olson *et al.*, 2009). The following spring several thousand gazelles were reported to stranded between the border fences of Russia and Mongolia where it was believed gazelles were attempting to cross into Russia to access a region of green grass at the start of the

growing season and at a period when the region was experiencing a long term decline in available biomass (Olson *et al.*, 2009). These observations and analysis highlights the threat to Mongolian gazelles by the development of infrastructure for natural resource extraction activities and the pending conflict if locations of critical habitat during seasonal extremes were to overlap with areas being developed (Olson *et al.*, 2009; Mallon & Jiang, 2009).

Behavioral Ecology

Outside of the rutting period, male and female Mongolian gazelles spend the majority (45%) of their time feeding (Bing-Wan *et al.*, 2009). During the rut, males dedicate their time to behavior associated with the rut or are lying down, an energy conservation strategy that carries into the post rut period (Bing-Wan *et al.*, 2009). Females did not vary their activity with respect to before, during, and post rut times (Bing-Wan *et al.*, 2009). Mongolian gazelles have one of the most synchronized birthing periods of all ungulate species with the majority of females giving birth in a 10 day period following the summer solstice (21 June) (Olson *et al.*, 2005b). Displaying behavior associated with 'hider' species, Mongolian gazelle calves spend their first 2 weeks mostly lying out motionless and apart from their mother (Odonkhuu *et al.*, 2009). However by 3-4 weeks of age calves are capable of moving with adults and begin to associate with large herds (Odonkhuu *et al.*, 2009).

Population Size

Commercial harvesting of gazelles began in 1932 and continued thru 1998 when it was banned by the Ministry of Nature and Environment (Reading *et al.*, 1998; Milner-Gulland & Lhagvasuren, 1998; WWF Mongolia). The total harvest of Mongolian gazelles decreased over time and this is believed to be a reflection of a declining population, although there are other variables that could explain the decline (Reading *et al.*, 1998). Household hunting in the mid and late 1990's was estimated to be 2 to 3 per family, and the total numbers of gazelles harvested for subsistence was estimated to be ~80,000 animals (Lhagvasuren & Milner-

Gulland, 1997; Reading *et al.*, 1998). There is currently no single wildlife management agency responsible for the management of the Mongolian gazelle population, but there have been calls for the creation of one (Reading *et al.*, 2006). Commercial harvesting as a management strategy is currently not an economically viable or sustainable option and anti-poaching measures needed to be strengthened (Zahler *et al.*, 2003).

Population trends were largely estimated from partial surveys or anecdotal evidence of population change; this has resulted in large fluctuations in estimates of the total population size (Leimgruber *et al.*, 2001; Milner-Gulland & Lhagvasuren, 1998; Reading *et al.*, 1998). For historical purposes and to provide targets for population recovery, it was estimated that as many as 4.5 million gazelle may have existed in Mongolia at the beginning of the 20th century (Milner-Gulland & Lhagvasuren, 1998).

In the mid 1990's, point estimates of the population varied between 400,000 and 2.7 million (unpublished 1994 air survey cited by: Milner-Gulland & Lhagvasuren, 1998; Reading *et al.*, 1998). Milner-Gulland and Lhagvasuren (1998) determined that none of the previous population surveys were likely correct, given the results of a population modeling exercise using historical harvesting data and available data on sex and age ratios. Olson *et al.*, (2005b) suggested that the population could likely recover quickly from population declines due to overhunting, given the high adult female fecundity (92%) and high first year survival (71%) of calves (Olson *et al.*, 2005b).

The use of long-distance driving transects following the protocol for Distance sampling and analysis was assessed by Olson *et al.*, (2005a) and they estimated approximately 870,000 gazelles to be in the southeastern 80,000-km² region of the steppe in Mongolia. This analysis did not include estimates for other portions of the range where gazelles are found in lower densities. Line transect sampling from vehicles was used to estimate the population of gazelles occupying the grassland region east of the Ulaanbaatar-Beijing railway in Mongolia and an estimate of 1.13 million (95% CI = 843,000 – 1.5 million) gazelles was reported (Olson *et al.*, in review). There was no detectable change in population size when comparing population estimates of overlapping study areas surveyed by

Olson *et al.* (2005). In this survey, Olson *et al.* (in review) found that Mongolian gazelle density was significantly influenced by the presence of just one household within 5 km's, even when forage conditions were considered ideal for Mongolian gazelles.

Conservation Status

The Tibetan antelope (*P. picticaudata*) is found in high altitude temperate grassland (up to 5,750 m a.s.l.) habitat throughout the Qinghai - Tibetan plateau, China, though a very small number (< 100 individuals) are found in Ladakh Province of India (Bhatnagar *et al.*, 2008; Schaller, 1998). In 1998 the total remaining population was estimated to be 100,000 (Schaller, 1998). The status of this species is Near Threatened (IUCN ver. 3.1) and threats to the species are 1) overhunting 2) competition with livestock 3) Fencing (Mallon & Bhatnagar, 2007).

The Przewalskii's gazelle (*P. przewalski*) is now found in 4 isolated populations around Qinghai Lake in Qinghai Province, China and the total adult population may be no more than 300 - 400 individuals (Runhua *et al.*, 2003). Habitat loss, extreme fragmentation due to fencing, low densities, and predation are the major threats to this species and they are listed as Critically Endangered (IUCN ver. 3.1) (Mallon, 2007).

Mongolian gazelles (*P. gutturosa*) are the most numerous of all three members of this genus and their global conservation status was assessed to be Least Concern (IUCN ver. 3.1) (Mallon, 2003). More recently, in the country with the largest remaining population (Mongolia) species, the status was recently assessed as Endangered (IUCN ver. 3.1) (Clark *et al.*, 2006). Economic development initiatives focusing on oil and mineral extraction, industrial hay cutting, and transport infrastructure threaten the integrity of large regions of the eastern portion of their range in Mongolia.

Humans have been pursuing Mongolian gazelles as a subsistence resource since at least the Upper Paleolithic period (Germonpre & Lbova, 1996). Since that period, the situation has intensified somewhat and a decline in population size was believed to have been reflected in a declining return from the former commercial harvest (Reading *et al.*, 1998). Unregulated

hunting figures could be as high as 250,000 animals/year (Wingard & Zahler, 2006).

Mongolia's rural population has increased since 1964 when records began identifying rural and urban populations separately (Milner-Gulland & Lhagvasuren, 1998). Aimags that were known to still have gazelles present had a statistically lower human population density than Aimags of where gazelles once occurred (Milner-Gulland & Lhagvasuren, 1998). This increase in human population density impacts gazelles in many ways ie. there are more potential hunters, greater abundance of livestock, and more domestic dogs which prey on gazelles (Young *et al.*, 2011).

Knowledge Gaps

Population dynamics. There has been little advance in the understanding of long term trends in the gazelle population. This is partly due to the fact that past methodologies used and areas surveyed have varied greatly which has prevented any direct comparison and assessment of trends. A lack of clear management objectives and adequate tools and support to develop a long term monitoring program has also limited advance in this area. Assessing such a population which demonstrates such a great deal variability with respect to group size and distribution over a large area presents a complicate challenge and one that would require a large amount of resources invested in determining appropriate methodologies and developing an adequately trained field crew.

In addition to trends in population size data on cause specific mortality, age and sex ratio of the adult population are not available. As the gazelle population is relatively large and spread out over a large area, this effort would require a great deal of dedicated effort and long term financial and political support. However, understanding population dynamics of Mongolian gazelle is a critical aspect for the sound conservation and management of the species.

Forage ecology with respect to nutritional requirements and preference. How gazelles perceive the forage available to them and what their foraging preferences are is still little known. Olson *et al.* (2010) pointed out that

a high proportion of the Mongolian steppe vegetation has below optimum levels of critical minerals such as Phosphorous (P), Calcium (Ca), and Magnesium (Mg). As a result, the authors postulate that in times of peak nutritional demand a gazelle would be unable to maintain phosphorous balance without being highly selective for species known to have higher concentrations of these minerals and thus seek out regions where forage conditions (high abundance of forbs and shrubs) meet these needs. Advancement in this area would assist in better understanding of habitat quality and its availability in time and space. In addition additional knowledge of gazelle forage preference and nutritional needs would help to helping to better define what ways gazelles and domestic livestock are competing with each other. With respect to calves and their nutritional uptake, knowledge of the quality of their mother's milk would be interesting to know.

Behavioral ecology. Scientific knowledge of how gazelles interact with each other and what important behaviors are displayed is limited. This is particularly evident with respect to rutting behavior and whether males hold harems or defend territories or use other cues to attract females. Another important time in a gazelle's life with respect to behavior is during and after calving and the importance of interaction between a calf and its mother. How often does a calf need to nurse and how and when does the mother wean the calf of its milk? How long does the bond between mother and calf last? What are the ways in which gazelles communicate with each other with respect to predator detection and alarms?

Predators and scavengers. We know very little about how and to what degree Mongolian gazelles are supporting predators and scavengers. With as many as a million gazelles (and previously presumably many more millions) gazelles are likely very important in supporting a diverse and healthy ecosystem. What is the importance of Mongolian gazelle moving nutrients across the steppe? In case of their decline and diminished role in ecosystem function, their loss would likely have a big impact and understanding their relationship with other species will help to better justify their conservation.

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References

- Abaturov, B. D., Dmitriev, I. A., Jargalsaikhan, L. & Omarov, K. Z. 2008. Phytomass utilization and deposition of feces by ungulates on steppe pastures of Eastern Mongolia. *Biology Bulletin*, 35: 302-309.
- Bing-Wan, L., Zhi-Qiang, Q., Bo, Z., Song-Tao, L., & Ming, L. 2009. Diurnal activity budgets and energy balance strategy of Mongolian gazelle (*Procapra gutturosa*) before, during and after the rut around Dalai Lake, Inner Mongolia. *Zoological Research*, 30: 694-698.
- Bhatnagar, Y. V., Seth, C.M., Takpa, J., Ul Haq, S., Namgail, T., Bagchi, S. & Mishra, C. 2008. A strategy for the conservation of the Tibetan gazelle *Procapra picticaudata* in Ladakh. *Conservation and Society*, 5: 262-276.
- Campos-Arceiz, A., Takatsuki, S. & Lhagvasuren, B. 2004. Food overlap between Mongolian gazelles and livestock in Omnogobi, southern Mongolia. *Ecological Research*, 19: 455-460.
- Clark, E. L., Munkhbat, J., Dulamtseren, S., Baillie, J. E. M., Batsaikhan, N., Samiya, R. & Stubbe, M. (compilers and editors). 2006. *Mongolian Red List of Mammals*. Regional Red List Series Vol. 1. Zoological Society of London, London.
- Deem, S. L., Karesh, W. B., Linn, M. J., Schaller, G., Lhagvasuren, B., Nyamsuren, N. & Olson K. 2001. Health evaluation of Mongolian gazelles *Procapra gutturosa* on the Eastern Steppes. *Gnusletter*, 20: 18-20.
- Frey, R. & Gebler, A. 2003. The highly specialized vocal tract of the male Mongolian gazelle (*Procapra gutturosa* Pallas, 1777 – Mammalia, Bovidae). *Journal of Anatomy*, 203: 451-471.
- Frey, R., Gebler, A., Olson, K. A., Odonkhuu, D., Fritsch, G., Batsaikhan, N., & Stuermer, I. W.

- 2008a. Mobile larynx in Mongolian gazelle: retraction of the larynx during rutting barks in male Mongolian gazelle (*Procapra gutturosa* Pallas, 1777). *Journal of Morphology*, 269: 1223-1237.
- Frey, R., Gebler, A., Olson, K. A., Odonkhuu, D., Fritsch, G., Batsaikhan, N. & Stuermer, I. W. 2008b. Head anatomy of Male and female Mongolian gazelle – A striking example of sexual dimorphism. In: *Anatomical Imaging: Towards a New Morphology*. Springer-Japan. 105 pp.
- Frey, R. & Riede, T. 2003. Sexual dimorphism of the Larynx of the Mongolian gazelle (*Procapra gutturosa* Pallas, 1777) (Mammalia, Artiodactyla, Bovidae). *Zoologischer Anzeiger*, 242: 33-62.
- Germonpre, M. & Lbova, L. 1996. Mammalian remains from the Upper Paleolithic site of Kamenka, buryatia (Siberia). *Journal of Archaeological Science*, 23: 35-57.
- Groves, C. P. 2000. Phylogenetic relationships within reent Antilopini (Bovidae). In: *Antelopes Deer, and Relatives*, S. Vrba and G. Schaller (eds.), pp. 223-233, Yale University Press, New Haven and London.
- Heptner, V. G., Nasimovich, A. A. & Bannikov, A. G. 1961. Mammals of the Soviet Union (V.G. Heptner and N.P. Naumov, eds.) Vysshaya Shkola, Moscow, Vol. 1. Artiodactyla and Perisodactyla. English edition R.S. Hoffman (Sci. ed.), Amerind Publ. Co., Pvt., Ltd., New Delhi, India.
- Ito, T. Y., Miura, N., Lhagvasuren, B., Enkhbileg, D., Takatsuki, S., Tsunekawa, A. & Jiang, Z. 2005. Preliminary evidence of a barrier effect of a railroad on the migration of Mongolian gazelles. *Conservation Biology*, 19: 945-948.
- Ito, T. Y., Miura, N., Lhagvasuren, B., Enkhbileg, D., Takatsuki, S., Tsunekawa, A. & Jiang Z. 2006. Satellite tracking of Mongolian gazelles (*Procapra gutturosa*) and habitat shifts in their seasonal ranges. *Journal of Zoology*, 269: 291-298.
- Jiang Z., Takatsuki, S., Zhongxin, G. & Kun, J. 1998. The present status, ecology and conservation of the Mongolian gazelle, *Procapra gutturosa*: a review. *Mammal Study*, 23: 63-78.
- Jiang, Z., Takatsuki, S., Li, J., Wang, W., Gao, Z. & Ma, J. 2002a. Seasonal variations in foods and digestion of Mongolian gazelles in China. *Journal of Wildlife Management*, 66: 40-47.
- Jiang, Z., Takatsuki, S., Li, J., Wang, W., Ma, J. & Gao, Z. 2002b. Feeding type and seasonal digestive strategy of Mongolian gazelles in China. *Journal of Mammalogy*, 83: 91-98.
- Jiang, Z., Takatsuki, S., Wang, W., Li, J., Jin, K. & Gao, Z. 2003. Seasonal changes in parotid and rumen papillary development in Mongolian gazelle (*Procapra gutturosa* Pallas). *Ecological Research*, 18: 65-72.
- Junsheng, L., Jianping, W. & Zhaowen, J. 1999. Food habits and selective grazing of Mongolian gazelle (*Procapra gutturosa*) in Hulunber Grassland. *Journal of Forestry Research*, 10: 187-190.
- Kholodova, M. V., Ryabinina, O., Lushchekina, A. A., Kiriliuk, V. E. & Neronov, V. M. 2002. Preliminary results of the genetic analysis of the Mongolian gazelle (*Procapra gutturosa* Pallas, 1777) Northern population. *Proceedings of the Institute of Biology*, 24: 163-169.
- Kuznetsova, M. V. & Kholodova, M. V. 2003. Molecular support for the placement of *Saiga* and *Procapra* in Antilopinae (Artiodactyla, Bovidae). *Journal of Mammalian Evolution*, 9: 271-279.
- Leimgruber, P., McShea, W. L., Brookes, C. J., Bolor-Erdene, L., Wemmer, C. & Larson, C. 2001. Spatial patterns in relative primary productivity and gazelle migration in the Eastern Steppes of Mongolia. *Biological Conservation*, 102: 205-212.
- Lhagvasuren, B. & Milner-Gulland, E.J. 1997. The status and management of the Mongolian gazelle *Procapra gutturosa* population. *Oryx*, 31: 127-134.
- Lux, E., Mix, H. M. & Zedev, B. 1997. *Damalinia (Tricholipeurus) zaganseeri*, n. sp. (Phthiraptera: Trichodectidae), a parasite from *Procapra gutturosa* (Artiodactyla: Bovidae) in Mongolia. *Journal of Medical Entomology*, 34: 599-604.
- Mallon, D. P. 2003. *Procapra gutturosa*. In: IUCN 2007. 2007 IUCN Red List of Threatened Species. <http://www.iucnredlist.org>. Downloaded on 09 April 2008.
- Mallon, D. P. 2007. *Procapra przewalskii*. In: IUCN 2007. 2007 IUCN Red List of Threatened Species. <http://www.iucnredlist.org>. Downloaded on 20 February 2008.
- Mallon, D. P. & Bhatnagar, Y. V. 2007. *Procapra*

- picticaudata*. In: IUCN 2007. 2007 IUCN Red List of Threatened Species. <http://www.iucnredlist.org>. Downloaded on 20 February 2008.
- Mallon, D. P. & Jiang, Z. 2009. Grazers on the plains: challenges and prospects for large herbivores in Central Asia. *Journal of Applied Ecology*, 46: 516-519.
- Milner-Gulland, E. J. & Lhagvasuren, B. 1998. Population dynamics of the Mongolian gazelle *Procapra gutturosa*: an historical analysis. *Journal of Applied Ecology*, 35: 240-251.
- Mueller, T. M. & Fagan, W. F. 2008. Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos*, 117: 654-664.
- Mueller, T. M., Olson, K. A., Dressler, G., Leimgruber, P., Fuller, T. K., Nicolson, C., Novaro, A., Bolgeri, M., Wattles, D., DeStefano, S., Calabrese, J., & Fagan, W. F. in press. How landscape dynamics link individual movements to population level patterns: a multispecies comparison of ungulate relocation data. *Global Ecology and Biogeography*.
- Mueller, T., Olson, K. A., Fuller, T. K., Schaller, G. B., Murray, M. G., & Leimgruber, P. 2008. In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *Journal of Applied Ecology*, 45: 649-658.
- Nyamsuren, D., Joly, D. O., Enkhtuvshin, S., Odonkhuu, D., Olson, K. A., Draisma, M. & Karesh, W. B. 2006. Exposure of Mongolian gazelles (*Procapra gutturosa*) to foot and mouth disease virus. *Journal of Wildlife Diseases*, 42: 154-158.
- Odening, K., Stolte, M., Lux, E. & Bockhardt, I. 1996. The Mongolian gazelle (*Procapra gutturosa*, Bovidae) as an intermediate host of three *Sarcocystis* species in Mongolia. *Applied Parasitology*, 37: 54-65.
- Odonkhuu, D., Olson, K. A., Schaller, G. B., Ginsberg, J.R. & Fuller, T.K. 2009. Activity, movements, and sociality of newborn Mongolian gazelle calves in the Eastern Steppe. *Acta Theriologica*, 54: 357-362.
- Olson, K. A., Fuller, T. K., Mueller, T. M., Murray, M. G., Nicolson, C., Odonkhuu, D., Bolortsetseg, S., & Schaller, G.B. 2010. Annual movements of Mongolian gazelles: Nomads in the eastern steppe. *Journal of Arid Environments*, 74: 1435-1442.
- Olson, K. A., Fuller, T. K., Schaller, G. B., Odonkhuu, D., & Murray, M. G. 2005a. Estimating the population density of Mongolian gazelles *Procapra gutturosa* by driving long-distance transects. *Oryx*, 39: 164-169.
- Olson, K. A., Fuller, T. K., Schaller, G. B., Lhagvasuren, B. & Odonkhuu D. 2005b. Reproduction, neonatal weights, and first-year survival of Mongolian gazelles (*Procapra gutturosa*). *Journal of Zoology*, 265: 227-233.
- Olson, K. A., Mueller, T., Bolortsetseg, S., Leimgruber, P., Fagan, W. F. & Fuller, T. K. 2009. A mega-herd of more than 200,000 Mongolian gazelles *Procapra gutturosa*: a consequence of habitat quality. *Oryx*, 43: 149-153.
- Olson, K.A., Mueller, T., Kerby, J.T., Bolortsetseg, S., Leimgruber, P., Nicolson, C.R., & Fuller, T.K. (in review). Death by a thousand huts? Effects of household presence on density and distribution of Mongolian gazelles. *Conservation Letters*.
- Olson, K. A., Mueller T., Leimgruber, P., Nicolson, C., Fuller, T. K., Bolortsetseg, S., Fine, A., Lhagvasuren, B. & Fagan, W. F. 2009. Fences impede long-distance Mongolian gazelle (*Procapra gutturosa*) movements in drought-stricken landscapes. *Mongolian Journal of Biological Sciences*, 7: 45-50.
- Olson, K. A., Murray, M. G., & Fuller, T. K. 2010. Vegetation composition and nutritional quality of forage for gazelles in Eastern Mongolia. *Rangeland Ecology and Management*, 63: 593-598.
- Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J. & Stenseth, N. C. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution*, 20: 503-510.
- Reading, R. P., Bedunah, D. J., & Amgalanbaatar, S. 2006. Conserving biodiversity on Mongolian rangelands: implications for protected area development and pastoral uses. USDA Forest Service Proceedings, RMRS-P-39: 1-17.
- Reading, R. P., Mix, H., Lhagvasuren, B. & Tseveenmyadag, N. 1998. The commercial harvest of wildlife in Dornod Aimag, Mongolia. *Journal of Wildlife Management*,

- 62: 59-71.
- Rebholz, W. & Harley, E. 1999. Phylogenetic relationships in the bovid subfamily Antilopinae based on mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 12: 87-94.
- Runhua, L., Zhiang, H. Zhigang, J. & Wenlong, Y. 2003. Phylogeography and genetic diversity of the critically endangered Przewalski's gazelle. *Animal Conservation*, 6: 361-367.
- Schaller, G. B. 1998. *Wildlife of the Tibetan Steppe*. University of Chicago Press, Chicago, IL, USA.
- Schaller, G. B., & Lhagvasuren, B. 1998. A disease outbreak in Mongolian gazelles. *Gnusletter*, 17: 17-18.
- Sharhuu, G. & Sharkhuu, T. 2004. The helminth fauna of wild and domestic ruminants in Mongolia – A review. *European Journal of Wildlife Research*, 50: 150-156.
- Sokolov, V. E. & Lushchekina, A. A. 1997. *Procapra gutturosa*. *Mammalian Species*, 571: 1-5.
- Sorokin, P. A., Kiriuluk, V. E. Lushchekina, A. A. & Kholdova, M. V. 2005. Genetic diversity of the Mongolian gazelle *Procapra gutturosa*, Pallas 1777. *Russian Journal of Genetics*, 41: 1101-1105.
- Wingard, J. R. & Zahler, P. 2006. *Silent Steppe: The Illegal Wildlife Trade Crisis in Mongolia*. Mongolia Discussion Papers, East Asia and Pacific Environment and Social Development Department. Washington D.C.: World Bank.
- Yoshihara, Y., Ito, T. Y., Lhagvasuren, B. & Takatsuki, S. 2008. A comparison of food resources used by Mongolian gazelles and sympatric livestock in three areas in Mongolia. *Journal of Arid Environments*, 72: 48-55.
- Young, J. K., Olson, K. A., Reading, R. P., Amgalanbaatar, S. & Berger, J. 2011. Is wildlife going to the dogs? Impacts of feral and free roaming dogs on wildlife populations. *Bioscience*, 61:125-132.
- Zahler, P., Olson, K., Khuukhenbaatar, G., Byamba, B., Schaller, G., Grigg, G., Pople, T., Payne, N., Draisma, M., Hopwood, P. & Odonkhoo, D. 2003. Management of Mongolian gazelles as a sustainable resource. *Mongolian Journal of Biological Sciences*, 1: 43-48.

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