Calving location selection patterns of saiga antelope in Mongolia

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Abstract

Habitat selection for calving by ungulates is an important behavioral trait because it affects neonate survival. Generally, ungulate calving site selection varies by vulnerability to predators, local topography, habitat quality and level of human disturbance. The Mongolian saiga (*Saiga tatarica mongolica*) is endemic to Mongolia where a threatened population of ~7000 exists in the northern Gobi Desert. We analyzed factors that could affect selection of saiga calving locations in the Sharga Nature Reserve, western Mongolia, using data obtained from ground surveys over 4 years between 2008 and 2012. Multiple factors explain calving location selection by saiga antelopes, based on the results of a generalized linear mixed model within a use availability framework. Individual saiga females preferred calving locations that were away from settlements and closer to water sources and avoided steeper slopes in comparison with random locations. These results demonstrate that the choice of calving locations for saiga antelope is driven by both internal and external factors. Understanding which factors influence calving location selection for saiga provides insights to protect important habitats.

Introduction

Variation in recruitment rate affects population trajectories of large herbivores (Gaillard *et al.*, 2000; Coulson, Gaillard & Festa-Bianchet, 2005). Juvenile survival of large herbivores is generally low and more variable relative to that of adults (Gaillard, Festa-Bianchet & Yoccoz, 1998); thus, investigating potential causes of recruitment variability is important for effective management of large herbivores, especially if the population size is small. Where predators are present, predation is the primary cause of neonatal mortality in large ungulates (Linnell, Aanes & Andersen, 1995). In response to the high risk of predation to neonates (Garrot, Bartmann & White, 1985), ungulates have evolved two main behavioral strategies, hiding or following (Estes, 1974; Lent, 1974; Leuthold, 1977), depending on whether the newborns lie concealed for their first few days or actively follow their mothers (Lent, 1974; Ralls, Kranz & Lundrigan, 1986). Following has been viewed as a strategy for avoiding predators in open habitats, while hiding is thought to reduce the predation risk in closed habitats (Estes, 1974; Lent, 1974).

Ungulate females often face challenges of selecting areas for calving that simultaneously provide sufficient forage to meet high energy demands of lactation and reduce exposure to predators (Lima & Dill, 1990; van Moorter *et al.*, 2009). Consequently, selection of calving areas by female ungulates reflects trade-offs between minimizing risk of predation and maximizing nutrition (Berger, 1992; Rachlow & Bowyer, 1998). Birth site selection of ungulates is also shaped by the need to reduce neonatal predation, including concealment cover (Barbknecht *et al.*, 2011; Pinard *et al.*, 2012), density of predators (Bergerud, Butler & Miller, 1984), topographic variables associated with visibility (Bowyer *et al.*, 1999; Mysterud & Ostbye, 1999) and experience in the previous year (Wiseman, Carling & Byers, 2006). In addition to the environmental factors, anthropogenic impacts such as proximity to settlements and roads can determine birth site selection of ungulate females (Berger, 2007; Singh *et al.*, 2010).

The Mongolia saiga (*Saiga tatarica mongolica*) is endemic to the semi-deserts of western Mongolia (Bannikov, 1954), with an estimated population of 7000 individuals (Young *et al.*, 2010), and is categorized as an endangered species by IUCN (Mallon, 2008). Like most ungulates, the saiga antelope segregate at the time of parturition and maternal females become solitary in late spring (e.g. end of May) to seek secluded areas for giving birth (Bekenov, Grachev &

Milner-Gulland, 1998). Newborns remain hidden for the first few days of life (Bannikov, 1954; Bekenov *et al.*, 1998). The life history of saiga is characterized by early female reproductive maturity, unusually large neonates relative to female body size and frequent twinning (Kuhl *et al.*, 2007; Buuveibaatar *et al.*, 2013*a*). Group size of Mongolian saiga is highly variable throughout the year and seasonality exerts strong effects, with the smallest groups forming in June (calving) and largest in December (Buuveibaatar *et al.*, 2013*b*). The calving period of Mongolian saiga is highly synchronous and most calving occurs over a short period (7–10 days) in early June; calves are highly vulnerable to predators (mainly raptors and foxes) during the first 2 months of life (Buuveibaatar *et al.*, 2013*a*).

Factors affecting calving site selection of saiga antelope (*Saiga tatarica*) are well documented in Kazakhstan, where saiga select sites with lower than average vegetation productivity, low interannual variation, intermediate distances from water sources and far from human settlements (Singh *et al.*, 2010). It is unknown if environmental and human variables similarly influence calving locations in the Mongolian subspecies, but such information would be useful for management of this endangered species (Clark & Javzansuren, 2006). Expansion of the existing reserves to protect key areas like calving grounds is recognized as a high priority for saiga conservation (Convention on Migratory Species, 2010).

Our goal herein is to identify factors that influence birth location selection of Mongolian saiga and assess the general relationship between spatial patterns of calving locations to habitat characteristics and thus areas in need of protection. We predicted that saiga would avoid higher elevations and steeper slopes during the calving period because these environmental traits increase predation risk to neonates (Bowyer, Kie & Van Ballenberghe, 1998). We also predicted that saiga females would prefer areas with high vegetation productivity to maximize energy gain (Bowyer *et al.*, 1999; Kie, 1999). During the birth period ungulates are highly sensitive to human disturbance as it reduces reproductive success (Phillips & Alldredge, 2000), so we expected calving locations to be located away from human settlements. Lastly, as availability of water is essential for lactating females (Singh *et al.*, 2010), we expected mothers to use areas closer to natural standing waters in this very dry region.

Study area

We studied saiga calving location selection in a 3000-km^2 part of the Sharga Nature Reserve (SNR) in western Mongolia (Fig. 1). The study area included ~30% of the entire Mongolian saiga range and is bounded by the Altai Mountains to the west. Elevations within the study area ranged from 1300 to 1900 m. The study area received ~100 mm precipitation annually and average air temperatures in summer and winter were 18 and −20°C, respectively (Buuveibaatar, 2011). The main human populations in the area are concentrated in soums (villages/towns). The abundance of livestock, particularly goats, in and adjacent to the SNR steadily increased over 30 years and now are the most dominant herbivores (Berger, Buuveibaatar & Mishra, 2013). The region is characterized by constant fluctuations in precipitation patterns resulting in a constant change in availability of quality forage (von Wehrden *et al.*, 2012). There is a lack of permanent surface water and local herders rely heavily on hand-drawn wells. A few alkaline lakes present near the towns are not potable for livestock and wildlife. Onions (*Allium* spp.), grasses (*Stipa*
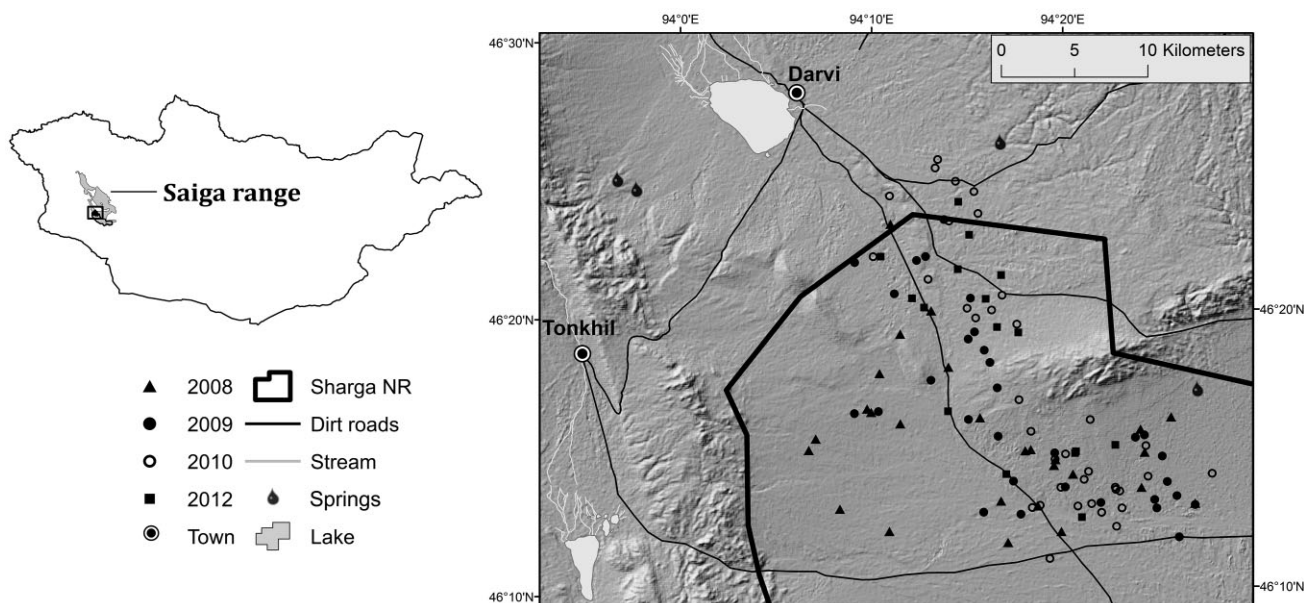
Figure 1 A map of study area and calving locations of saiga antelope observed during 2008–2012 in western Mongolia. The box in a country map denotes the 'Study site'.

spp.) and anabasis *Anabasis brevifolia* are the most common plants in this region (Buuveibaatar, Gunbat & Fuller, 2012). Some shrubs (*Caragana* spp.) and trees, such as saxaul *Haloxylon ammodendron*, are sparsely distributed. Common predators in this system are red foxes *Vulpes vulpes*, corsac foxes *V. corsac* and raptors such as golden eagles *Aquila chrysaetos* and cinereous vultures *Aegypius monachus* (Buuveibaatar *et al.*, 2013a).

Materials and methods

We conducted extensive searches across the SNR to determine spatial distribution of pregnant females prior to calving, as a part of saiga calf survival research during 2008–2010 and 2012 (Buuveibaatar *et al.*, 2013a). Observations of pregnant females were made during the early morning and late evening, when saiga were most active. Systematic searches for newborn calves also were conducted when we observed females exhibiting distinct postpartum behavior. We identified calving locations based on direct observation of births, newborn calves or by presence of common calving location characteristics, including placenta and disturbed or cleared vegetation in a circular pattern. Geographical coordinates (Universal Transverse Mercator, UTM; zone 46N) were recorded with a Garmin GPS 60CSX unit (with ±3 m error; Garmin International Inc., Kansas City, KS, USA) at each location where calving was observed.

Defining used and available habitat

A major difficulty in assessing habitat use concerns the definition of available habitat. This becomes problematic, especially when quantifying used relative to theoretically available areas (Hjermann, 2000). For this study, we operationally defined 'used habitat' as the location of each observed calf birth. The number of calving locations recorded for saiga population in the SNR in different years during 2008–2010 were 27, 31 and 36, respectively (Table 1); due to a shorter field season in 2012, we recorded only 16 calving locations. To

define available habitat we, created minimum convex polygons (100% MCP) based on all observations of calving locations for each year to delineate the extent of a yearly calving area within which we could sample random points (Table 1). Random locations were separately sampled from within each of the yearly calving areas (2008 – 30, 2009 – 30, 2010 – 40, 2012 – 20) to fulfill assumptions of the use and availability framework (Manly *et al.*, 2002). There is no established rule to decide the minimum sample sizes for random points (Peng, Lee & Ingersoll, 2002); however, we tried to keep our samples symmetric (e.g. equal number of used and random points).

Spatial landscape features

Spatial landscape feature values for used and random calving locations were calculated using ArcMap 10.2 and Erdas Imagine 2010 (Leica Geosystems GIS & Mapping, LLC, Heerbrugg, Switzerland). We calculated six spatial landscape features for each used and random location: vegetation productivity, elevation, slope, and distances to nearest surface water and town. Vegetation productivity was estimated using the normalized difference vegetation index (NDVI) acquired by the moderate resolution imaging spectroradiometer on board the TERRA satellite. For each survey period, we obtained a 16-day NDVI composite in 250-m resolution from NASA's Earth Observing System Gateway (http://reverb.echo.nasa.gov) and re-projected the data to the UTM (zone 46 N). Elevation values for the locations were extracted from a 30-m resolution digital elevation model (DEM). We used the surface tool in spatial analyst toolbox to create a slope raster map from the DEM. Using extraction tool in the spatial analyst toolbox, we also extracted NDVI, slope and elevation values for each used and random location. The nearest Euclidean distances to surface water and towns were calculated for each used and random location point using the proximity tool in the analysis toolbox in ArcMap 10.2 (Environmental System Research Institute, Redlands, CA, USA). Spatial distribution of natural standing water was mapped using data collected during the study period and a GIS database of Gobi-Altai province.

Statistical analysis

To examine spatial patterns of saiga calving locations, average nearest neighbor (ANN) function of spatial statistics toolbox in the ArcMap 10.2 was used to calculate Euclidean distance between calving locations for each year. The nearest neighbor index is expressed as the ratio of the observed mean distance to the expected mean distance. The expected distance is the average distance between neighbors in a hypothetical random distribution. If the index (*Z*-value) is <1, the pattern exhibits clustering; if the index is >1, the trend is toward uniform dispersion. Annual relationships between nearest neighbor distances of calving locations, density of calving locations and vegetation productivity (e.g. the mean NDVI value of the calving areas for each year) were tested using linear regression (Montgomery & Pack, 1982).

Table 1 Number of saiga calving locations (single: twin), the average nearest neighbor (ANN) distances among calving locations, extent of calving areas (100% MCP), density of calving locations/km², average (±SD) NDVI value (non-normalized) within the calving areas during 2008–2012 in the Sharga Nature Reserve, western Mongolia

Year	Number of calving locations	ANN, m	Calving area, km²	Density of calving location #/km²	NDVI value, mean ± SD
2008	27 (13:14)	2189	343.4	0.079	926.7 ± 252.5
2009	31 (22:9)	1755	279.2	0.111	875.8 ± 213.7
2010	35 (34:1)	1558	270.8	0.129	743.2 ± 202.1
2012	16 (12:4)	2366	155.0	0.103	699.7 ± 125.9
Average	27 (20:7)	1986	251.9	0.107	811.3 ± 198.5

MCP, minimum convex polygons; NDVI, normalized difference vegetation index; SD, standard deviation.

We used a generalized linear mixed model (GLMM) with a binomial error distribution to test for differences between saiga calving and the random locations. We quantified the collinearity among the environmental and human-associated covariates using the Pearson's rho and did not include within the same model strongly correlated covariates (rho ≥0.6). Elevation was excluded from the model because it was negatively correlated with distances to town (rho = −0.67) and positively correlated with NDVI (rho = 0.59). Therefore, our final model included four explanatory variables including NDVI, slope and distance to nearest town (town) and surface water (water). The second-order polynomial ($y \sim x + x^2$) was used to test all variables because a similar study has shown saiga females selected for intermediate values due to various trade-offs (e.g. Singh *et al.*, 2010). Because second-order polynomial models were not significant for all variables, we eliminated them and the model was re-run in the non-polynomial form ($y \sim x$). The GLMM was run with the library 'lme4' (Bates, Maechler & Bolker, 2011) in R statistical software (R Development Core Team, 2014), with year as a random term. We ran all possible model subsets of the four variables and ranked them using the Akaike information criterion for small sample sizes (AICc). The final set of models was the most parsimonious based on ΔAICc < 4 (Anderson, 2008). Models with a ≤ 2 AICc unit difference (e.g. ΔAICc = AICc$_i$ − minAICc) were considered equivalent (Burnham & Anderson, 2002). To quantify the influence of each covariate on calving location selection, we used model-averaging techniques to obtain parameter estimates, unconditional standard errors and the relative support of each variable (Burnham & Anderson, 2002) within the 'MuMIn' library in R (Barton, 2012). In addition, the model AICc weights were calculated to measure the likelihood of a candidate model being the best among the set of fitted models. We used the area under the receiver operating characteristic curve (AUC) to measure the discrimination ability of the final models, with 0.5 showing no discrimination ability and 1.0 showing perfect discrimination ability of a model (Pearce & Ferrier, 2000).

Results

During 2008–2010 and 2012, we collected data on calving locations for 28 females that produced twins and 81 females that produced single calves, for a total of 109 calving locations (Fig. 1; Table 1). Calving areas ranged from 115 to 343 km² with densities of 0.08–0.14 calving locations/km² (Table 1). The ANN distances between calving locations, pooled for 4 years, averaged 1986 ± 351 m and was largest in 2012 and smallest in 2010 (Table 1). Calving locations were randomly distributed in 2009 ($Z = 0.29$, $P = 0.77$) and 2010 ($Z = 0.31$, $P = 0.97$), and highly dispersed patterns were observed in 2008 ($Z = 5.18$, $P < 0.001$) and 2012 ($Z = 4.08$, $P < 0.001$). Overall (e.g. cumulatively across all years), spatial distribution of calving locations was clustered ($Z = −3.08$, $P < 0.001$). There was no relationship between NDVI and the ANN distance between calving locations ($R^2 = 0.001$, $F = 0.003$, $P < 0.960$, $n = 4$) or between density of calving locations and NDVI ($R^2 = 0.35$, $F = 1.115$, $P = 0.401$) during 2008–2012.

Table 2 Top ranked models (ΔAICc ≤ 4.0) on basis of minimum AICc explaining difference in calving locations versus random sites in Sharga Nature Reserve, western Mongolia during 2008–2012

Model structure	LogLik	AICc	ΔAICc	Weights
water + NDVI + slope + town	−133.11	278.60	0.00	0.57
water + slope + town	−134.79	279.81	1.21	0.30

AICc, corrected Akaike information criterion; Delta AICc, difference between model AICc and the minimum AICc; LogLik, log likelihood; NDVI, normalized difference vegetation index; Weights, model AICc weight.

Table 3 Model-averaged parameter estimates of the full model for determining calving location selection of saiga antelope relative to available locations during 2008–2012, western Mongolia

	Estimate	SE	Z	P	Variable importance
Intercept	1.077	0.708	1.521	0.128	
Distance to water	−0.249	0.051	4.861	0.000***	1.00
Slope	−0.184	0.082	2.229	0.025*	1.00
Distance to town	0.126	0.027	4.674	0.000***	1.00
NDVI	1.325	0.725	1.827	0.067	0.65

Random effect: Year, SD = 1.364e-06. Model-averaged estimates, adjusted standard errors and relative importance of variables were obtained based on the Akaike information iriterion for small samples sizes (AICc) statistic following Burnham & Anderson (2002) model-averaging procedures.
NDVI, normalized difference vegetation index; SE, standard error.

Calving location selection of individual saiga females was best explained by a mixed model that included the factors of NDVI, slope, distances to nearest water and distances to towns (Table 2). The exclusion of a covariate of NDVI from the best model produced the second-ranked competitive model (e.g. ΔAICc value was 1.21). These two models accounted for ~87% of the AICc weight among the 16 possible subset models (Table 2). Model-averaged parameter estimates of the full model suggests that parturient saiga females preferred locations that were farther from a town and closer to surface water (e.g. avoided farther distances from water), and avoided areas with steeper slopes (Table 3). By contrast, the NDVI variable emerged as a nonsignificant predictor affecting saiga calving location selection (Table 3). Among the top models (e.g. models ΔAICc ≤ 4), distances to nearest town, surface water and slope were always included and consequently have maximum relative variable importance values (e.g. the relative importance of these variables was 1.0%), whereas the relative importance of NDVI was 0.65% (Table 3). The AUC for the final averaged model was 0.81, indicating good discriminate ability.

Discussion

In some years, the distribution of calving locations was dispersed across the calving area during the parturition period. Dispersing over large areas to distance themselves from other

parturient females during calving season may be a strategy to enhance calf survival by reducing the risk of predation (Bergerud *et al.*, 1984; Bowyer *et al.*, 1999). We suspect that such unpredictable distribution of calving locations reduces search efficiency by predators by creating gaps across the landscape (McCauley, Wilson & de Roos, 1993). Perhaps dispersion is a good anti-predation strategy for Mongolian saiga females during calving period because density is low. In contrast, population densities of saiga antelope are much higher in Kazakhstan where they form large aggregations to give birth, perhaps a predator-swamping strategy to minimize neonate mortality. It remains unclear whether the dispersion of birth locations has a strong effect on saiga calf survival in Mongolia.

As we predicted, saiga calving locations were situated away from towns relative to available sites. The saiga calving sites in Kazakhstan were also located away from settlements (Singh *et al.*, 2010). Singh *et al.* (2010) suggested that this response was likely due to intensity of poaching (Kuhl *et al.*, 2009), but law enforcement appears stronger in Mongolia (Chimeddorj, 2009). Instead, pasture depletion due to livestock grazing is a serious problem in Mongolia (Wesche *et al.*, 2010; Berger *et al.*, 2013), and levels of grazing show strong geographical variation with high impact areas near settled areas (Batkhishig & Lehmkuhl, 2003). Consequently, heavily grazed areas in proximity to settlements may have insufficient forage for lactating females or provide less cover for saiga calves and increase exposure to predators. Alternatively, saiga may avoid settlements because free-ranging dogs of livestock herders kill saiga neonates (Buuveibaatar, Young & Fine, 2010).

Access to water is a critical factor for large herbivores inhabiting arid environments (Bleich, Marshal & Andrew, 2010), particularly for lactating females during the calving period. The saiga calving sites were located in an intermediate distance from nearest source of water in Kazakhstan (Singh *et al.*, 2010), suggesting a trade-off between predation, disease, or disturbance risk and water requirements during parturition (Bowyer *et al.*, 1999; Milner-Gulland *et al.*, 2001; Morgan *et al.*, 2005). However, in our study, calving locations were located closer to surface water in comparison with available habitat. Many rangeland studies have reported that the impacts of concentrated grazing by livestock near the water sources on vegetation dynamics generally lead to marked reductions in forage resources (Fernandez-Gimenez & Allen-Diaz, 2001; Stumpp *et al.*, 2005). The density of livestock herders is lower in summer (e.g. during calving season) in the study area as they move up to the mountains (Buuveibaatar *et al.*, 2010). It is possible that low level of human disturbance and competition with livestock for resources allows saiga females to use areas close to surface water during the calving period.

Of all the variables measured, vegetation productivity (e.g. NDVI) had the smallest effect on selection of calving locations. Habitat choices of ungulates are associated with vegetation communities with distinctive nutritional properties (Wilmshurst *et al.*, 1999) because nutrition level of plants affects growth rate and subsequent survival of neonates (Cook *et al.*, 2004). Experimental study suggests that without

selecting for forage plants that have high concentrations of minerals, saiga antelope in semi-desert range cannot meet their nutritional requirements for weight gain and lactation (Abaturov & Subbotin, 2011). Regions abundant with forbs and shrubs that have significantly greater concentrations of calcium, phosphorous and magnesium are important for Mongolian gazelles in Eastern Mongolia, especially shortly before and immediately after calving (Olson, Murray & Fuller, 2010). Choice of saiga calving locations therefore is likely constrained by spatial distribution of vegetation communities that have high nutritional value. Future research should put more emphasis on calving location selection behavior at finer scales in relation to vegetation quality, rather than quantity indexed as NDVI.

We used individually observed, multiyear calving locations to determine their spatial patterns and identify factors influencing calving location selection of saiga in western Mongolia. Our findings have shown that the choice of calving locations for saiga antelope is driven by both internal and external factors. Understanding which factors affect calving location selection patterns of Mongolian saiga offers insights for prioritizing habitats for protection.

Acknowledgments

References

Abaturov, B.D. & Subbotin, A.E. (2011). Forage quality thresholds for saiga antelope in a semi-desert rangeland. *Rus. J. Theriol.* **10**, 71–81.

Anderson, D.R. (2008). *Model based inference in life sciences. A primer on evidence*. New York: Springer.

Bannikov, A.G. (1954). *Mammals of the Mongolian People's Republic*. Moscow: Publishing House of the Academy of Sciences of USSR.

Barbknecht, A.E., Fairbanks, W.S., Rogerson, J.D., Maichak, E.J., Scurlock, B.M. & Meadows, L.L. (2011). Elk parturition site selection at local and landscape scales. *J. Wildl. Mgmt.* **75**, 646–654.

Barton, K. (2012). Package 'MuMIn'. Model selection and model averaging based on information criteria. R package version 1.7.11.

Bates, D., Maechler, M. & Bolker, B. (2011). Package 'lme4'. Linear mixed-effects models using S4 classes. R package version 1.1–5.

Batkhishig, O. & Lehmkuhl, F. (2003). Degradation und desertifikation in der mongolei. *Petermanns Geogr. Mitt.* **147**, 48–49, (in Germany).

Bekenov, A.B., Grachev, I.A. & Milner-Gulland, E.J. (1998). The ecology and management of the saiga antelope in Kazakhstan. *Mammal Rev.* **28**, 1–52.

Berger, J. (1992). Facilitation of reproductive synchrony by gestation adjustment in gregarious mammals: a new hypothesis. *Ecology* **73**, 323–329.

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Lett.* **3**, 620–623.

Berger, J., Buuveibaatar, B. & Mishra, C. (2013). Globalization of the cashmere market and the decline of large mammals in Central Asia. *Conserv. Biol.* **27**, 679–689.

Bergerud, A.T., Butler, H.E. & Miller, D.R. (1984). Antipredator tactics of caribou: dispersion in mountains. *Can. J. Zool.* **62**, 1566–1575.

Bleich, V.C., Marshal, J.P. & Andrew, N.G. (2010). Habitat use by a desert ungulate: predicting effects of water availability on mountain sheep. *J. Arid Environ.* **74**, 638–645.

Bowyer, R.T., Kie, J.G. & Van Ballenberghe, V. (1998). Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? *J. Mammal.* **79**, 415–425.

Bowyer, R.T., Van Ballenberghe, V., Kie, J.G. & Maier, J.A.K. (1999). Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. *J. Mammal.* **80**, 1070–1083.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information – theoretic approach*, 2nd edn. New York: Spring-Verlag.

Buuveibaatar, B. (2011). *Factors affecting survival and cause-specific mortality of saiga calves* (Saiga tatarica mongolica) *in Mongolia*. Thesis, University of Massachusetts Amherst.

Buuveibaatar, B., Young, J.K. & Fine, A.E. (2010). Mongolian saiga in Sharga Nature Reserve: are domestic dogs a threat to saiga? *Mong. J. Biol. Sci.* **7**, 37–43.

Buuveibaatar, B., Gunbat, G. & Fuller, T.K. (2012). Food habits and dietary overlap among livestock and saigas in Mongolia. *Saiga News* **14**, 14–16.

Buuveibaatar, B., Young, J.K., Berger, J., Fine, A.E., Lkhagvasuren, B., Zahler, P. & Fuller, T.K. (2013*a*). Factors affecting survival and cause-specific mortality of saiga calves in Mongolia. *J. Mammal.* **94**, 127–136.

Buuveibaatar, B., Fuller, T.K., Fine, A.E., Chimeddorj, B., Young, J.K. & Berger, J. (2013*b*). Changes in grouping patterns of saiga in relation to intrinsic and environmental factors in Mongolia. *J. Zool. (Lond.)* **291**, 51–58.

Chimeddorj, B. (2009). Conservation of the saiga antelope in the Great Lakes Basin of western Mongolia. *Saiga News* **10**, 12–13.

Clark, E.L. & Javzansuren, M. (2006). Saiga tatarica. In *Mongolian red list of mammals*: 64–68. Clark, E.L., Javzansuren, M., Dulamtseren, S., Baillie, J.E.M., Batsaikhan, N., King, S.R.B., Samiya, R. & Stubbe, M. (Eds). London: Zoological Society of London.

Convention on Migratory Species. (2010). *Medium term international work programme for the saiga antelope* (2011–

2015). Second Meeting of the Signatories to the Memorandum of Understanding Concerning Conservation, Restoration and Sustainable Use of the Saiga Antelope, Ulaanbaatar. Available at: http://www.cms.int

Cook, J.G., Johnson, B.K., Cook, R.C., Riggs, R.A., Dilcurto, T., Bryant, L.D. & Irwin, L.L. (2004). Effects of summer–autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monogr.* **155**, 1–61.

Coulson, T., Gaillard, J.M. & Festa-Bianchet, M. (2005). Decomposing the variation in population growth into contributions from multiple demographic rates. *J. Anim. Ecol.* **74**, 789–801.

Estes, R.D. (1974). Social organization of the African Bovidae. In *The behavior of ungulates and its relation to management*: 166–205. Geist, V. & Walther, F. (Eds). Morges: IUCN.

Fernandez-Gimenez, M. & Allen-Diaz, B. (2001). Vegetation change along gradients from water sources in three grazed Mongolian ecosystems. *Plant Ecol.* **157**, 101–118.

Gaillard, J.M., Festa-Bianchet, M. & Yoccoz, N.G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* **13**, 58–63.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* **31**, 367–393.

Garrot, R.A., Bartmann, R.M. & White, G.C. (1985). Comparison of radio-transmitter packages relative to deer fawn mortality. *J. Wildl. Mgmt.* **49**, 758–759.

Hjermann, D.O. (2000). Analyzing habitat selection in animals without well-defined home ranges. *Ecology* **81**, 1462–1468.

Kie, J.G. (1999). Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *J. Mammal.* **80**, 1114–1129.

Kuhl, A., Mysterud, A., Erdnenov, G.I., Lushchekina, A.A., Grachev, I.A., Bekenov, A.B. & Milner-Gulland, E.J. (2007). The 'big spenders' of the steppe: sex-specific maternal allocation and twinning in the saiga antelope. *Proc. R. Soc. Lond. B.* **274**, 1293–1299.

Kuhl, A., Balinova, N., Bykova, E., Arylov, Y.N., Esipov, A., Lushchekina, A.A. & Milner-Gulland, E.J. (2009). The role of saiga poaching in rural communities: linkages between attitudes, socio-economic circumstances and behaviour. *Biol. Conserv.* **142**, 1442–1449.

Lent, P.C. (1974). Mother–infant relations in ungulates. In *The behaviour of ungulates and its relation to management*: 14–55. Walther, F. (Ed.). Morges: IUCN.

Leuthold, W. (1977). *African ungulates: a comparative review of their ethology and behavioral ecology*. New York: Springer Verlag.

Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619–640.

Linnell, J.D.C., Aanes, R. & Andersen, R. (1995). Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biol.* **1**, 209–223.

Mallon, D.P. (2008). Saiga tatarica. *The IUCN Red List of Threatened Species*. Version 2014.2. Available at: www.iucnredlist.org.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002). *Resource selection by animals statistical design and analysis for field studies*, 2nd edn. Norwell: Kluwer Academic Publishers.

McCauley, E., Wilson, W.G. & de Roos, A.M. (1993). Dynamics of age-structured and spatially structured predator–prey interactions: individual-based models and population-level formulations. *Am. Nat.* **142**, 412–442.

Milner-Gulland, E.J., Kholodova, M.V., Bekenov, A.B., Bukreeva, O.M., Grachev, I.A., Amgalan, L. & Lushchekina, A.A. (2001). Dramatic declines in saiga antelope populations. *Oryx* **35**, 340–345.

Montgomery, D.C. & Pack, E.A. (1982). *Introduction to linear regression analysis*. New York: John Wiley & Sons.

van Moorter, B., Gaillard, J.M., McLaughlin, P.D., Delorme, D., Klein, F. & Boyce, M.S. (2009). Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales. *Oecologia* **159**, 669–678.

Morgan, E.R., Shaikenov, B., Torgerson, P.R., Medley, G.F. & Milner-Gulland, E.J. (2005). Helminths of saiga antelope in Kazakhstan: implications for conservation and livestock production. *J. Wildl. Dis.* **41**, 148–161.

Mysterud, A. & Ostbye, E. (1999). Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildlife Soc. B.* **27**, 385–394.

Olson, K.A., Murray, M.G. & Fuller, T.K. (2010). Vegetation composition and nutritional quality of forage for gazelles in Eastern Mongolia. *Rangeland Ecol. Mgmt.* **63**, 593–598.

Pearce, J. & Ferrier, S. (2000). Evaluating the predictive performance of habitat models developed using logistic regression. *Ecol. Model.* **133**, 225–245.

Peng, C.Y.J., Lee, K.L. & Ingersoll, G.M. (2002). An introduction to logistic regression analysis and reporting. *J. Educ. Res.* **96**, 3–14.

Phillips, G.E. & Alldredge, A.W. (2000). Reproductive success of elk following disturbance by humans during calving season. *J. Wildl. Mgmt.* **64**, 521–530.

Pinard, V., Dussault, C., Ouellet, J.P., Fortin, D. & Courtois, R. (2012). Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. *J. Wildl. Mgmt.* **76**, 189–199.

R Development Core Team (2014). *A language and environment for statistical computing*. Vienna: R Foundation for statistical computing.

Rachlow, J.L. & Bowyer, R.T. (1998). Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. *J. Zool. (Lond.)* **245**, 457–465.

Ralls, K., Kranz, K. & Lundrigan, B. (1986). Mother–young relationships in captive ungulates: variability and clustering. *Anim. Behav.* **34**, 134–145.

Singh, N.J., Grachev, I.A., Bekenov, A.B. & Milner-Gulland, E.J. (2010). Saiga antelope calving site selection is increasingly driven by human disturbance. *Biol. Conserv.* **143**, 1770–1779.

Stumpp, M., Wesche, K., Retzer, V. & Miehe, G. (2005). Impact of grazing livestock and distance from water source on soil fertility in Southern Mongolia. *Mt Res. Dev.* **25**, 244–251.

von Wehrden, H., Hanspach, J., Kaczensky, P., Fischer, J. & Wesche, K. (2012). Global assessment of the non-equilibrium concept in rangelands. *Ecol. Appl.* **22**, 393–399.

Wesche, K., Ronnenberg, K., Retzer, V. & Miehe, G. (2010). Effects of large herbivore exclusion on southern Mongolian desert steppes. *Acta Oecol.* **36**, 234–241.

Wilmshurst, J.F., Fryxell, J.M., Farm, B.P., Sinclair, A.R.E. & Henschel, C.P. (1999). Spatial distribution of Serengeti wildebeest in relation to resources. *Can. J. Zool.* **77**, 1223–1232.

Wiseman, P.A., Carling, M.D. & Byers, J.A. (2006). Frequency and correlates of birth-site fidelity in pronghorns (*Antilocapra americana*). *J. Mammal.* **87**, 312–317.

Young, J.K., Murray, K.M., Strindberg, S., Buuveibaatar, B. & Berger, J. (2010). Population estimates of Mongolian saiga: implications for effective monitoring and population recovery. *Oryx* **44**, 285–292.