**Understanding snow leopard populations and their spatial ecology through Spatial Capture Recapture Analysis across three sites in South Gobi, Mongolia**

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**Abstract**

Accurate estimates of ecological state variables such as population density provide key metrics for monitoring population changes over time in response to changes in environmental conditions or protection regimes. Changes in populations can be defined in terms of habitat use, abundance or distribution. One can define habitat use as a hierarchical process in terms of species distribution, home range placements within the distribution range, and space use within the home range. Snow leopards are known to have large home ranges, several hundreds km2 in size. They also have strong spatial preferences for certain habitats where patches of suitable habitats can often be smaller than individual home range sizes. Density is often also strongly correlated with the habitat quality and with availability of prey, whereas individuals’ movements, and hence detection are associated with availability of markable sites or sites with critical resource such as water bodies.

We investigate the effect of environmental variables on snow leopard populations across three sites with somewhat different environments, using camera trap data. We present estimated density surfaces based on ecologically relevant covariates and investigate similarities and differences in how density depends on the covariates across the three sites. While we find differences in average density per site, our results indicate that density depends on ruggedness covariate in the same way across the sites irrespective of their protection regime. Differences in the average density of each site can be explained by differences in the amount of suitable habitat in each site.

As regards individuals’ habitat use, our best model included ‘compensatory heterogeneity’ (Efford and Mowat 2014) between range and intercept parameters of detection functions, suggesting that animals moving in larger ranges were less likely to be detected at their activity centres and vice-versa. Our results also suggest that animals with activity centres near water-bodies had smaller ranges and higher detection probabilities, but this relationship varied between the three regions. Similarly, traps in canyons were more likely to have detected snow leopards compared to those on ridgelines or steppe. Estimated snow leopard density ranged from nearly 0 to 5 per 100 km2, depending on location. Camera traps are often placed at locations where encounter rates are expected to be highest, and often not placed where they are expected to be low. This results in over-sampling of high density regions and positive bias in density and abundance if the spatial variation in density is not taken into account in analysis. Our results show that in the hierarchical order of habitat selection, availability of suitable habitat governs abundance of snow leopards, where they tend to be robust in their selection at the level of their activity ranges, but are more sensitive to differences at the level of space use within activity ranges.

**Introduction**

Understanding spatial population ecology and habitat use of animals and plants is critical for effective management and conservation of biodiversity (Lawton 1993). Accurate estimates of ecological state variables such as population density provide key metrics for monitoring changes over time in response to changes in environmental conditions or as a result of conservation actions. These estimates also help determine long-term viability of populations and conservation strategies. Habitat use by species on the other hand is a hierarchical process (ref. XX) that can be defined at several levels. Range level selection defined by species distribution is considered as the first order selection, which is governed by general habitat suitability and connectivity (ref. XX). The second order selection can be defined as the home range placements within the distribution range, and is generally affected by localized conditions of habitat suitability, food availability and other anthropogenic factors (ref. XX). The third order selection is considered as space use within the home range and often has nuances where components of a habitat are used at a finer scale, often as a function of a series of movements within the activity range (ref. XX).

Snow leopards are known to have large home ranges of the order of 80-700 km2 in size (Johansson et al., 2016). Studies indicate that they have strong spatial preferences to certain habitats where individual contiguous habitat patches can often be smaller than the known individual home range sizes. Less than 2% of the global snow leopard range has ever been sampled using systematic camera trapping or genetic sampling for population estimation (SLSS 2014). Difficult terrain, harsh environments and large spatial scales have historically made estimating snow leopard populations notoriously challenging (Jackson et al. xx). Most of these challenges however have been largely alleviated through revolutionary technological advances such as remote cameras (Karanth et al. XX; Sharma et al. 2014; O’Connell et al., 2011, Bischof et al., 2014) and non-invasive genetics (Beja‐Periera et al., 2009, Janecka et al., 2011) that allow sampling of populations using a statistical framework that takes into consideration imperfect detection by estimating detection probability. Few studies have been conducted at scales large enough to provide reliable estimates of snow leopard populations and their trends, let alone provide information about the spatial patterns of distribution of populations within or across landscapes.

Spatial Capture Recapture (SCR) methods to estimate wildlife population density and size of wildlife populations were first introduced by Efford (2004), and have developed rapidly since (Borchers and Efford 2008; Royle and Young 2008; Sutherland and XX 2014). Royle et al. (2013) provided a detailed review and introduction to SCR methods, while Borchers and Fewster, (2016) provided an updated review and speculated on future developments. Sollman et al (2012) propose that spatial capture recapture models perform well with relatively smaller sampled areas, as long as they are similar or larger than the extent of individual movement during the study period. However, in case of uneven use of habitat, most of the times these smaller sampling sites end up being chosen in areas that are most likely to record snow leopards (high encounter rate of snow leopard signs and scrapes), which in turn are likely to produce biased results unless variability incurred by habitat types is incorporated in the analysis. Because snow leopard habitat is typically highly structured with strong preferences and avoidances (e.g. high and low altitudes, steppe, human settlements etc.), two SCR developments of particular importance for analysis of snow leopard data are (1) methods for modelling non-uniform activity centre density (Borchers and Efford, 2008) and (2) methods for modelling non-uniform detectability and effective range as a function of habitat where animals with greater ranges are likely to have lower probability of being detected by traps placed at their activity centres (ref. XX). Inferences assuming uniform effective area of their activity range around activity centres can address the heterogeneity in density as due to habitats. Effective area of range around activity centers can be a surrogate for variability in trap rates and can thus be modelled as a function of habitat characteristics representing trapping locations.

In SCR analysis, a state space is defined as an area where the sampling is done for estimating animal abundance and density. Selection of state spaces is done based on the a priori information about the distribution of the species, and hence represents the first order selection. Spatial capture recapture methods provide an opportunity to explore process-based conceptual framework for studying species’ spatial ecology at the second and third order of selection. The density models can be defined by an inhomogeneous point process model describing the distribution of activity centres within a particular landscape. Detection models on the other hand help understand space use within a home range, and thus reflect the third order of selection. The spatial capture-recapture analyses thus provide a statistical modelling framework for not only estimating species’ density, but also studying its spatial ecology and facilitate comparison between the above parameters between multiple sites and/or periods.

Our study areas (sites) represent three different protection regimes: strictly protected, community conserved and marginally protected areas. Our analyses explored the effects of habitat covariates on detection probability, range sizes and ultimately snow leopard density between these three sites. We considered a range of candidate models and present abundance estimates for the three sites by model-averaging the top ranking models. We present density surfaces based on ecologically relevant covariates and use information theoretic approach to compare the three sites for snow leopard density. In addition to improving our ecological understanding of snow leopard behaviour, density and hierarchical habitat use, our results provide a framework to compare snow leopard densities across space and time while addressing the issue of non-homogenous space use.

**Methodology**

***Study Area***

South Gobi province in Mongolia comprises of important snow leopard habitats (fig 1, map of snow leopard distribution). The area is characterized by rugged mountain ranges interspersed with vast stretches of steppe. The area has low human density of XX people per km2, and relatively high livestock density of XX heads per km2. Since 2008, the Snow Leopard Trust and Snow Leopard Conservation Foundation have been conducting a long-term snow leopard study in the Tost Mountains of South Gobi. These mountains are partially protected through community based conservation programs such as Snow Leopard Enterprises and Livestock Insurance programs operational since 19XX and 2009 respectively (ref. XX). Recently, the mountain range has been designated a Protected Area by the Government of Mongolia. The snow leopard population of Tost is being monitored through camera trapping since 2009 (Sharma et al., 2014), and 24 snow leopards have been monitored through GPS telemetry since 2008 (Johansson et al. XX). In the year 2013, the camera trapping work was expanded to two neighbouring sites, viz. Nemegt Mountain complex, and Noyon Mountain range. Noyon Mountains are marginally protected as they have had a community based conservation program operational until the year 20XX. The communities still value their engagement with conservation organizations, even though there are XX operational mines extracting coal and XX in Noyon since the year XX. Nemegt Mountains on the other hand represent the strictly Protected Area of Gurvan Saikhan National Park. No human land-use other than research and protection patrols are allowed in the area, but illegal trespassing and poaching are likely to be an issue just like anywhere else. The three Mountain ranges are separated by several kilometres of steppe (fig 1). Although camera trapping over several years has revealed emigration and immigration of individuals between them, within a trapping season characterized by 2-3 months, we found no evidence of any interaction between these three populations.

***Sampling for data collection***

Digital camera traps (ReconyxTM) with a combination of infrared and motion sensors to detect animal movement, and low-glow monochrome illumination were used to sample snow leopard populations. The number of cameras varied between 30 and 40, depending on the availability of suitable snow leopard habitat that ranged from 920 to 1200 km2. We used networking approach to place cameras in the field every 1-3 km from another nearby camera. Precise camera trap locations were identified by surveying 2-5 km on foot in the mountains around each potential location, searching for locations where possibility of capturing snow leopards was high. This was achieved by looking for spots with fresh snow leopard signs identifiable as scrapes or fresh urine markings. Most camera trap locations were characterized as saddles on ridgelines, overhanging rocks or steep canyon walls where snow leopards tend to mark and scrape. While we found ample fresh signs to identify the best sites for installing camera traps in the community conserved and strictly protected sites; there were fewer snow leopard signs in the unprotected site, and we identified the best locations for installing camera traps based on intuition and knowledge of snow leopard natural history from other sampling sites. All cameras were left in the field for an average of 105.45 (SE=11.81), 50.47 (SE=4.44) and 89.89 (SE=2.44) days in the community conserved (Tost), strictly protected (Nemegt) and marginally protected (Noyon) sites respectively. It took between 7-20 days to set up camera traps in the field, and nearly half the time to collect them. Each camera’s set up date and operational history were used to determine effort and its effect on the probability of detecting snow leopards.

***Data preparation***

Each sequence of snow leopard recorded on a camera separated by at least 5 minutes was recorded as a unique encounter in the database. Data on cubs following mothers were discarded for this analysis to avoid biases arising from data duplication. Individuals were identified from each encounter following methods described by Sharma et al. (2014). Encounters where snow leopards could not be identified from up to three similarities or differences in patterns were discarded from analysis. Each trap was characterized by the value of terrain ruggedness at its specific location to within 90m. Additionally, we recorded topography of the trap location as saddle, steppe or canyon, and marked presence/absence of a waterhole within 50m of the camera traps. All but binary covariates’ data were centred and scaled to have a mean of 0 and standard deviation 1 to make the model fits more stable.

**Demarcation of sampling extent (state space) and identifying habitat covariates**

Snow leopards are known to use rugged mountains and tend to avoid flat steppe (Johansson et al. 2015). We estimated terrain ruggedness index (Riley et al., 1999) using digital elevation model of the study area at a resolution of 90m. We generalized terrain ruggedness index by recreating the raster of terrain ruggedness using focal statistic tool (ArcGIS) for a circular neighbourhood of 500 meters to be used as a covariate (“stdGC”) that may have influenced snow leopard density. To characterize habitats, we used logistic regression on 35,000 telemetry locations representing 20 adult snow leopards, using terrain ruggedness index (Riley et al., 1999) as dependent variable. We then chose regions with estimated probabilities greater than 0.5 as the habitat likely to be used by snow leopards, creating a binary snow leopard habitat variable (“stdBC”) with 1 representing snow leopard habitat and 0 denoting non-habitat. We identified contiguous habitats defined as snow leopard habitat and created polygons for contiguous patches of rugged mountains. We included all rugged patches in the sampling polygon as long as the distance between two rugged patches was less than 15 km. This was done on the basis of telemetry data defining median maximum linear distance moved by snow leopards in a day’s time. For patches that had no neighbouring rugged patches within 15 km, a hard boundary was demarcated at the edge of the mountain base. This was done following knowledge generated from telemetry data where snow leopards are known to generally not venture out in habitats that cannot be covered within a day’s time.

***Data analysis***

We used the R package secr (Efford, 2016) to fit density surface models to the three sampled sites by maximum likelihood. SCR models have two component models: a model for encounter rate and a model for activity centre density. The encounter rate model has three sub-models: a range model determining how far form their activity centres animals are encountered, an intercept model determining the encounter rate at the activity centre, and an effective area model determining the effective area of the animals’ ranges. Each of these models may be made to depend on spatial or non-spatial covariates. We assumed no temporal effect on detection probability of snow leopards during the sampling period primarily because the study periods were restricted to a single season during each sampling session. Our earlier analyses using conventional capture recapture methods did not indicate any temporal effects on capture probability too. Therefore, we considered the entire sampling as a single occasion and session (ref. XX).

Candidate model sets were developed for the sampled sites to investigate the differential effects of various covariates potentially influencing snow leopard behaviour, ecology and natural history. We investigated models with various combinations of covariates for the density model, the intercept model, and the range model. The general forms of the density model, intercept model and range model, respectively, are as follows:

(1)

(2)

(3)

where

is the *d*th spatially referenced covariate at location ***s*** that affects density (*D*), and and are the density intercept parameter and *d*th regression parameter (all covariates were treated as known, notwithstanding the fact that stdGC and stdBC had been estimated);

is the *l*th covariate that affects expected encounter rate at distance zero (), and and are the intercept parameter and *l*th regression parameter for expected encounter rate at distance zero;

is the *i*th covariate that affects the range parameter (), and and are the range intercept parameter and *i*th regression parameter.

Models were ranked based on minimum AICc, which balances the improved fit due to use of more parameters against the increased variance due to use of more parameters (Burnham et al., 2010). We only consider models with cumulative AICc weights greater than 0.95.

The frequency with which a snow leopard encounters a camera trap is likely to be affected by the ruggedness and topography of the sites at which the camera traps are installed, the ruggedness and topography in other parts of its range, and whether or not the camera trap is close to a water hole. Similarly, individuals with smaller effective range are more likely to be encountered at their activity centres as opposed to those with bigger effective ranges. We investigated the effect of terrain ruggedness, topography and presence of waterholes on the expected encounter rate intercept and range parameter.

Conventional SCR analyses assume uniform density across the study areas and do not model spatial variation in density at resolutions finer than survey regions or strata. We investigated the dependence of snow leopard densities on terrain ruggedness, estimating non-uniform density surface that depends on terrain ruggedness in the three study regions, using Equation (1) above. Since sampling was conducted in different sites and seasons, we expected detection probabilities and ranging areas to be affected by covariates differently.

We fitted models to all three regions simultaneously to investigate whether covariate effects were shared across the three regions. A combination of models were run testing various interactions between covariates and the three study sites. We use information theoretic approach to report differences (or lack of) in densities as a function of habitat covariates and conservation status between the three study sites, while also explicitly testing the effects of covariates on detection probability and ranging areas. While we tested standard additive and interactive models where density and detection were a function or covariates; to test if the difference in density between the three sites is a function of the difference in available habitats, we formulated models by using mean value of the habitat suitability, its deviation from the mean at each point and site (see table XX for model formulations).

**Results**

We obtained 54, 99 and 86 adult snow leopards encounters respectively on camera traps (fig 1, camera trap layout) from strictly protected, community conserved and marginally protected sampling sites. We ran a total 22 models using a combination of covariates affecting density, detectability and range size by the snow leopard. The top 2 models had a cumulative AIC weight of 0.97, indicating strong evidence in favour of these model parameters defining most variability in the data (Table XX). The top two models had AICc value within 2 AIC values, therefore we used model averaging to generate the predicted density surface and abundance estimates from the three sites. The top models had density vary as a function of ruggedness, but was not affected by the differences between the three sites. Our top models chose a0 parameterization for detection probability indicating that the range size was a function of covariates, i.e. animals moving in bigger ranges were less likely to be detected at their activity centres and vice versa. The effect of water and topography on effective ranging area (and detectability) interacted with the sites, thus indicating different relationships between water and detectability across the three sites (table XX). Traps around water-bodies had smaller effective area of ranging and higher detection probabilities, but this relationship varied between the three regions. Similarly, traps in canyons were more likely to have detected snow leopards as compared to those on ridgelines or steppe.

Greater ruggedness resulted in higher density uniformly across the three study sites. Models that used variation in density as a function of difference between the available habitat to snow leopards did not rank high, thus indicating that density was similar across the three sites, at least during the period analysed here. Although mean snow leopard densities in the three study sites were 0.71, XX and 0.75 per 100 km2, modelled density of activity centres ranged between 0.0XX to nearly 5.XX per 100 km2  within the study areas.

**Discussion**

Snow leopard is a habitat specialist and mountain ranges such as the ones in South Gobi provide a highly structured habitat with variable patch sizes to the species. They tend to prefer rugged habitats and avoid plain steppe in Gobi. Some recent studies have used spatial capture recapture for snow leopards (Alexander et al., 2016, Kumar XX), but the analyses have been limited to small study areas that assume uniform activity centre density models and patterns of space use without taking into account the heterogeneity of the habitat. In heterogeneous habitats, failing to address the effect of habitat suitability on density can lead to positive bias or higher variance, thus making comparison between snow leopard densities across time and/or space less informative. While design based inference by collecting data from sufficiently large number of traps representing all habitat variability equally can be used; since each camera station has significant cost implications, it is less productive for researchers to install as many cameras in spots that are clearly in less suitable snow leopard habitat.

Within their distribution range (first order selection), snow leopards’ activity centres in landscapes are likely to be distributed as a function of habitat covariates. Activity ranges (second order selection) might be exclusive for territorial individuals, but populations of large felids generally are constituted of territorial, transient and floater individuals from both sexes, with the latter two categories leading to substantial overlaps (Chundawat et al., 2016; Johansson et al., 2016). In South Gobi, terrain ruggedness defined spatial variation in density within study areas (Table xx). Density varied sharply between non-habitats (flat terrain) and highly suitable habitats (more rugged terrain) thus presenting a strong case against small sampling sites which can bias the density estimates of snow leopard populations from a region unless selected randomly or modelled through appropriate covariates.

Snow leopards are reported to have preferences for certain micro-habitats for scraping and marking with urine (third order selection). These sites are often used to collect camera trapping and genetic data (e.g. ref. XX). Our results also suggested strong effects of certain micro-habitats on detection probability and underscore that camera placement can have a strong effect on the estimated detection functions. Sites with water-holes affected the expected range area (a0), but its effect was differential between the three sites. This could be likely because some areas were sampled during the summer, whereas others were sampled in autumn and winter. Effect of topography on the expected range area (a0 in the model that compared all study areas showed that snow leopards were more likely to be encountered in canyons as opposed to ridgelines and steppe (Table 2).

Snow leopards tend to have large home ranges. Protected Areas that can encompass viable populations of the species need to be large, but the number of such areas is limited (Johansson et al XX). The Global Snow Leopard and Ecosystem Protection Program has identified 23 snow leopard landscapes to be protected by 2020. Some State owned Protected Areas focus on strict protection by limiting human use, others implement participatory community based conservation programs (GSLEP 2013, Mishra XX). Given the scale of its distribution that could be spread up to nearly 2 million km2, a large proportion of snow leopard habitat may not have any protection either through an on-going conservation program or as a protected area. The protection strategies may vary across, sometimes even within landscapes, depending on the local situation analysis. Ultimately, all snow leopard conservation programs aim at either improving or maintaining the snow leopard densities. Comparing overall abundances or absolute densities between sites can be misleading as the abundance is likely to be related to the extent of suitable habitat available to the species in a particular site. Our study provides a framework to compare populations between sites while simultaneously addressing the effect of spatial variables on density, detection and range sizes.

The survey in Noyon (marginally protected) resulted in detection of few signs of snow leopards’ presence while setting up camera traps, but we had several snow leopard encounters and the density was similar to the other two areas. It is important to note that sign surveys can sometimes be misleading in their ability to detect real changes in snow leopard populations. While it is likely that there is a behavioral shift in the snow leopards using the marginally protected area, thus resulting in fewer scrapes and urine markings, it is also possible that we missed out detecting their presence due to an overall smaller number of 'markable' sites. The results highlight the importance of empirically estimating detection probability even when using sign surveys to even report presence (or absence) of snow leopards.

The study was conducted across three neighbouring sites with different protection regimes. Although ultimately we are interested in the abundance of snow leopards in an area, more often than not it is also likely to be a function of the extent of available suitable habitat in each site. Our results show that there was little evidence of any difference in the snow leopard densities across the three sites, thus denoting not much difference in the second order habitat selection. However we found strong evidence of differences in the way the snow leopards used habitat at the third order of selection across the three sites.

While it is encouraging that snow leopards are still surviving in habitats with differential conservation statuses, our field surveys had revealed signs of poaching, trapping and disturbance from mining in the site with marginal protection. It is likely that the populations could be undergoing vigorous changes (see Sharma et al. 2014) and hence be susceptible to sudden collapse as has been seen in other carnivores (e.g. Chundawat and Gruisen, 20XX). It is therefore important to sample the populations systematically over a period of time to monitor densities, sex ratios and population dynamics.

Although new, some of the methods being used in this paper have been available to practitioners for a few years now (J A Royle et al., 2013). However, lack of appropriate design and analytical guidelines that can expose users to the full potential of the spatial capture recapture analyses have seemingly restricted their application in snow leopard habitats. Our results highlight the importance of analysing data collected in the capture-recapture framework using ecologically meaningful covariates that can affect the detection probability, spatial ranging patterns, and density within and across study areas. We emphasize the importance of estimating density of snow leopards by investigating a series of models based on the species’ natural history and ecology, specifically the density, detection probability and range size to compare densities across a cross section of time and/or space. In addition to understanding ecological and conservation specific nuances of snow leopard densities, we provide an application of the analytical framework to compare densities across multiple study areas or periods. Variants of the candidate model set used here can be employed to analyse data when reporting and comparing snow leopard populations from one or more study areas.

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Table 1 Models based on minimum AICc from the three study areas analysed individually and together. Models are described using the syntax of program secr: “~1” means the RHS of Equations (1) to (3) contains only an intercept term; fitted; “~x” means that it contains an intercept and covariate “x”; “~x+y” means that it contains an intercept and covariates “x” and “y”. The number of parameters in the model is denoted “npar” and the log likelihood “logLik”. The difference between the AICc and the minimum AICc for the given Site is dAICc, while the associated weight is AICcwt. Explanatory variables are as follows: “stdGC” is a standardised continuous variable quantifying terrain ruggedness; “Topo” is a topography factor with levels “canyon”, “ridgeline” and “steppe”; “Water” is a binary variable indicating whether or not a camera was within 50m of a water source; “session” is a factor variable indexing site; “rmeanGC” is XX; and “rmeanGCdev” defines XX. Parameter D represents density of activity centres; a0 describes effective ranging area; and sigma represents XX.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Model** | **npar** | **logLik** | **AICc** | **dAICc** | **AICcwt** |
| D~stdGC a0~Topo + Water \* session sigma~1 | 11 | -490.267 | 1011.637 | 0 | 0.6772 |
| D~stdGC a0~Water \* session sigma~1 | 9 | -494.721 | 1013.249 | 1.612 | 0.3025 |
| D~stdGC a0~Topo sigma~1 | 6 | -502.449 | 1019.369 | 7.732 | 0.0142 |
| D~stdGC a0~Water + Topo sigma~1 | 7 | -501.825 | 1021.043 | 9.406 | 0.0061 |
| D~stdGC a0~Topo + session sigma~1 | 8 | -500.752 | 1022.003 | 10.366 | 0 |
| D~stdGC a0~Water sigma~1 | 5 | -506.669 | 1025.052 | 13.415 | 0 |
| D~stdGC + session a0~Topo sigma~1 | 8 | -502.438 | 1025.375 | 13.738 | 0 |
| D~1 lambda0~session sigma~1 | 5 | -507.924 | 1027.561 | 15.924 | 0 |
| D~1 lambda0~1 sigma~1 | 3 | -511.177 | 1029.004 | 17.367 | 0 |
| D~stdGC \* session a0~Topo sigma~1 | 10 | -502.42 | 1032.174 | 20.537 | 0 |
| D~session lambda0~session sigma~session | 9 | -504.829 | 1033.465 | 21.828 | 0 |
| D~rmeanGC + rmeanGCdev:session + session lambda0~Topo sigma~1 | 11 | -502.42 | 1035.944 | 24.307 | 0 |
| D~stdGC a0~Topo \* session sigma~1 | 12 | -500.431 | 1036.005 | 24.368 | 0 |
| D~stdGC + session a0~session sigma~session | 10 | -504.404 | 1036.141 | 24.504 | 0 |
| D~stdGC a0~Topo \* session sigma~session | 14 | -497.828 | 1039.811 | 28.174 | 0 |
| D~stdGC \* session a0~session sigma~session | 12 | -504.393 | 1043.929 | 32.292 | 0 |
| D~session a0~Topo \* session sigma~session | 15 | -497.772 | 1044.744 | 33.107 | 0 |
| D~rmeanGC + rmeanGCdev:session + session lambda0~session sigma~session | 13 | -504.393 | 1048.268 | 36.631 | 0 |
| D~stdGC + session a0~Topo \* session sigma~session | 16 | -497.745 | 1050.156 | 38.519 | 0 |
| D~stdGC + session a0~Topo \* session sigma~session | 16 | -497.745 | 1050.156 | 38.519 | 0 |
| D~rmeanGCdev \* session lambda0~Topo \* session sigma~1 | 16 | -500.321 | 1055.308 | 43.671 | 0 |
| D~rmeanGCdev \* session lambda0~Topo \* session sigma~session | 18 | -497.474 | 1062.038 | 50.401 | 0 |

Table 2 Coefficients of parameters and estimates of snow leopard abundance from the three study areas, based on the best site-specific models and the null models. Parameters are as shown in Equations (1) to (6), but with subscripts indicating explanatory variables as follows: “stdGC” is a standardised continuous variable quantifying terrain ruggedness; “stdBC” is a standardised binary variable for habitat suitability; “Water is a binary variable indicating whether or not a camera was within 50m of a water source. The submodel that the parameter relates to is indicated in brackets in the “Parameter” column.

|  |  |  |  |
| --- | --- | --- | --- |
| Parameter | Top model Coefficient | LCL | UCL |
| (*D*) | -9.55 | -9.88 | -9.22 |
| (*D*) | 0.11 | -0.39 | 0.6 |
|  | 6.36 | 5.88 | 6.84 |
|  | -0.07 | -0.72 | 0.58 |
|  | -0.37 | -0.78 | 0.05 |
|  | -19.43 | -19.43 | -19.43 |
|  | 0.29 | -0.09 | 0.67 |
|  | 0.1 | -0.43 | 0.62 |
|  | -0.12 | -1.04 | 0.80 |
|  | 1.89 | 0.97 | 2.81 |
| () | 8.97 | 8.86 | 9.08 |

Figure 1: Study Area and Snow Leopard Distribution (inset). + denote camera locations, and shades denote standardized terrain ruggedness covariate

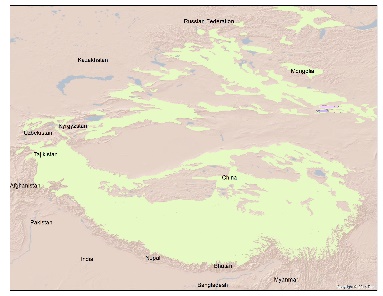


Figure 4: Snow leopard density surface based on the model averaged estimates

