**Improving ecological inferences about snow leopard populations from Spatial Capture Recapture Analysis**

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**Abstract**

(to come…xx)

**Introduction**

For effective management and conservation of biodiversity, it is critical that we understand the spatial population ecology of animals and plants (Lawton 1993). 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 as a result of conservation actions. These estimates also help determine long-term viability of populations and conservation strategies. However, for elusive, low density, and wide-ranging species like the snow leopard, difficult terrain, harsh environments and large spatial scales makes estimating population density notoriously challenging (Jackson et al. xx).

Most of these challenges have been largely alleviated through revolutionary technological advances such as remote cameras (Karanth et al. XX; Sharma et al. XX; 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 populations using a statistical framework that takes into consideration imperfect detection by estimating detection probability.

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). A large part of this can be blamed on difficult terrain and the sparse densities of snow leopards in areas they inhabit (e.g. Jackson et al., 1995). It is only recently that technological advancements have made it possible to sample snow leopards using camera traps in study areas that are large enough for the purpose of robustly estimating and monitoring populations (Sharma et al., 2014). Yet, few studies have been conducted at scales that are large enough (e.g. several times animals’ home range sizes) to infer snow leopard population sizes or population dynamics without risking misinterpretations caused by small sampling areas (e.g. Williams et al. XX). Even then, most studies have used conventional capture recapture analyses that require ad hoc estimation of effective sampling area, and hence detection probability, and which may lead to inaccurate density estimates (ref. XX). It is only in the last one decade that Spatial Capture Recapture (SCR) methods have been developed to estimate wildlife population densities by modelling the inherent spatial nature of the sampling process and the populations being sampled (Borchers and Efford 2008; Royle and Young, 2008).

Spatial Capture Recapture (SCR) methods to estimate wildlife population density and size in 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. These developments have made it possible to estimate and monitor snow leopard populations, yet to-date, few studies have been conducted at scales large enough to provide reliable estimates of populations and their trends, let alone provide information about the spatial patterns of distribution of populations within or across landscapes.

Snow leopards are known to have large home ranges of the order of 250-700 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. Inferences assuming ranging patterns around activity centres that do not take into account habitat types could lead to biases. Similarly, not accounting for variability in trap rates as a function of certain habitat characteristics may also result in biases. Ranges 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 large scale overlaps (Chundawat et al., 2016; Johansson et al., 2016). Density of a species on the other hand is often strongly correlated with the habitat quality and availability of prey. Analyses that assume constant density across large study areas can lead to spurious inferences in case density is inherently varying spatially.

Because snow leopard habitat is typically highly structured, 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 space usage, by means of least-cost path distances ( Royle et al., 2013; Sutherland et al., 2015). Most SCR models assume that expected encounter rate depends on the Euclidean distance between detector and activity centre, but in a highly structured environment this may not be appropriate. For example, leopards may have more encounters with a distant trap than a closer trap if the habitat between distant trap and activity centre is more conducive to movement than that between the closer trap and the activity centre. To accommodate this phenomenon, Royle et al. (2013) and Sutherland et al. (2015) proposed replacing Euclidian distance with a least-cost path distance in which movement cost depends on the kind of habitat the movement is through. The method involves estimation of movement cost parameter(s) simultaneously with other SCR parameters. Sutherland et al. (2015) demonstrated that violations of the Euclidean assumption can bias estimates of density and they suggest that least-cost distance is preferable in highly structured landscapes.

Snow leopards tend to have large home ranges. Protected Areas that can encompass viable populations need to be large, but the number of such areas is limited. 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 XX, Mishra XX). A large proportion of snow leopard habitat however may not have any on-going specific conservation models. The protection strategies may vary across or even within each landscape, depending on the local situation analysis. Ultimately, all snow leopard conservation models aim at either improving or maintaining the snow leopard densities, where density is often a function of availability of quality of habitat to a species. Few studies provide a comparison between the impacts of different conservation strategies on snow leopard conservation, let alone address the effect of spatial variables on density, detection and ranging patterns.

Our study areas represent three different protection regimes: strictly protected, partially protected and unprotected areas. Our analyses explore the effects of habitat covariates on detection probability, ranging patterns and ultimately snow leopard density and abundance. We consider a range of candidate models and present abundance estimates from the best model, along with spatially variable density surfaces based on ecologically relevant covariates such as ruggedness, topography and presence of waterholes. We also report the densities between the three study areas and compare them using information theoretic approach.

We investigate the effect of not modelling the effects of covariates and of not modelling least-cost distance in analysis of camera trapping data using SCR methods. In addition to improving our ecological understanding of snow leopard behaviour and density, our results provide a set of generic guidelines for the analysis of snow leopard populations in mountain habitats and a framework to compare snow leopard densities across space (or time).

**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 sq km, and relatively high livestock density of XX heads per sq km. 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 has been monitored through camera trapping since 2009 (Sharma et al., 2014). In the year 2013, the camera trapping work was expanded to two neighbouring areas, viz. Nemegt Mountain complex, and Noyon Mountain range. While Noyon Mountains are largely unprotected and have XX operational mines extracting coal and XX, they have had a community based conservation program operational until yearXX. Nemegt Mountains on the other hand represent the strictly Protected Area of Gurvan Saikhan National Park. 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 sq km. 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 sites where possibility of capturing snow leopards was high. This was achieved by looking for sites 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 partially and fully protected sites; there were fewer snow leopard signs in the unprotected area, and we identified the best sites for installing camera traps based on intuition and knowledge of snow leopard natural history from other sampling areas in the region. 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 partially protected, strictly protected and unprotected habitats 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 to enable analysis based on times.

***Data preparation***

We obtained 54, 99 and 86 adult snow leopards encounters respectively on camera traps (fig 1, camera trap layout) from strictly protected partially protected and unprotected sampling areas. Data on cubs following mothers were discarded for this analysis. 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 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 standard deviation 1 to make the model fits more stable.

**Demarcation of sampling mask and identifying habitat covariates**

Snow leopards are known to use rugged mountains and tend to avoid flat terrain (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 point statistic tool (ArcGIS) for a circular neighbourhood of 500 meters to be used as a covariate that may have influenced snow leopard density. This variable is called “stdGC below”.) 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 (called “stdBC” below) 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 areas 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 two sub-models: a range model (determining how far form their activity centres animals are encountered) and an intercept model (determining the encounter rate at the activity centre). Each of these models may be made to depend on spatial or non-spatial covariates. When least-cost path distance is used, this allows the range parameter of the encounter rate function to vary depending on the habitat that the animal moves through. 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 each sampled area separately to investigate for each area the effects of various covariates that may influence 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;

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.

In addition, the non-Euclidian distance between two adjacent points and is modelled as

(4)

where is the Euclidian distance between the two points,

(5)

(6)

and and are the *m*th spatially referenced covariate at locations and that determine the cost of moving between these two points, while is the assocaited regression parameter. With this parameterisation, the larger , the greater the cost of moving due to the *m*th covariate.

The above non-Euclidian distance metric is different from that used by Royle et al. (2013) and Sutherland et al. (2015). They used . We found that their parameterisation resulted in high correlation between and with our data, and poor estimation precision for . Our parameterisation increases the contrast between noneuc values at different values of , and results in a model with suitably low correlations between these parameters.

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 discarded models with the lowest cumulative AIC weight up to 0.05 (5%).

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 home range, and whether or not the camera trap is close to a water hole. We investigated the effect of terrain ruggedness, topography and presence of waterholes on the expected encounter rate intercept and range parameter.

Telemetry data from 20 snow leopards, obtained separately from this study, showed that their habitat use appeared to be strongly influenced by selection for rugged habitat types and avoidance of flat. In order to incorporate the effect of habitat-dependent ranging patterns, we considered models using least-cost path distance in addition to models with Euclidian distance (which assume that ranging pattern is unaffected by the habitat that the animal moves through).

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 each study area, using Equation (1) above.

We also fitted models to all three areas simultaneously and used AICc to investigate whether covariate effects were area-specific or shared across areas. We used this analysis to report differences (or lack of) in densities between the three study areas.

For the purposes of comparison, we provide plots of both the estimated density surface in each survey area, and the predicted density, conditional on capture histories, from a model with a flat density surface model (using the secr function ``fx.total’’). The latter are often misinterpreted as density surface models; we plot them here to illustrate the difference between them and density surface models.

**Results**

The best models by AIC were found to differ between the three study areas (Table 1). Non-uniform space use with movement cost affected by ruggedness and with density dependent on habitat were the top models in case of each study area. Having fitted such a models and estimated the cost of movement as a function of ruggedness, it is possible to find the estimated least-cost path between any points in the survey region.

Additional support for these models was provided by the fact that the least-cost paths between separate high usage regions traversed exactly the routes between them that had been identified from the telemetry data (see Fig. 2a, for example). On the basis of a habitat ruggedness covariate, the fitted models reproduced the connectivity patterns that had been expected prior to analysis, even though no information on connectivity itself was provided to the model. The estimated cost function parameters () in the cases of Tost and Noyon have signs that indicate that in Tost and Noyon, those parts of the survey region that are classified as not rugged (stdBC=0) on not as “conductive” (i.e. facilitate movement less) than in parts that are classified as rugged (stdBC=1). This coincides with the a proiri expectation that snow loepards prefer to be in rugged regions. By contrast, the sign of the estimated cost function parameter in Nemegt () indicates that parts of the survey region with low ruggedness (low stdGC) have higher “conductance” (facilitate movement more) than parts with high ruggedness. This is believed to reflect the different nature of the Nemegt survey region compared to Tost and Noyon. Unlike the latter two, Nemegt is comprised of small islands of rugged terrain separated by large “seas” of flat terrain. The islands are too small to contain leopards entire home ranges, so that leopards move long distances through flat terrain to access other bits of rugged terrain. This longer movement through flat terrain is reflected in higher “conductance” of this terrain.

Density estimates varied with habitat each of the three study areas. Topography affected the expected encounter rate at distance zero from an activity centre () in case of strictly protected and partially protected study areas, whereas water affected it in the strictly protected area, which was sampled in the summer. The effect of water was marginal on the expected encounter rate at distance zero from activity centre in the unprotected and partially protected study areas that were sampled in winter and autumn respectively.

The estimated conditional probability density function of activity centre locations and our estimated density surface based on habitat covariates produced starkly different maps (Fig. 4a & 4b). The latter is a valid representation of activity centre distribution.

Population abundance estimates for the most parsimonious models differed from the estimates from “null” models (assuming flat density, no effect of covariates on encounter rates and ranging patterns unaffected by any covariates (Table XX)) by between 7% and 31%. Each of the top models have AICc values at least ?? smaller than those of the corresponding null models. The best models by AICc all have AICc weights accounting for at least 95% of the total AICc weights of all models considered..

Mean snow leopard densities in the three study areas ranged between 0.57xx (95% CI =0.56-0.68) per 100 km2 in the unprotected, to 0.69 (95% CI = 0.66-0.88) per 100 km2 in the partially protected, and 0.93 (95% CI = 0.68-2.06) per 100 km2 in the strictly protected study area. It is important to note that these differences also reflect the amount of snow leopard habitat available to snow leopards in each of the study areas. The best model (by AICc) fitted to all three areas simultaneously, assuming that the effects of covariates on , , and noneuc are the same across the three areas, but allowing density to vary between areas, has an AICc value 197 greater than the combined AICc value for the best models for each separate area. It therefore has no support by AICc, and we base inference of models fitted separately to each area. (Table XX AIC).

**Discussion**

Snow leopard is a habitat specialist and mountain ranges such as the ones in South Gobi provide a highly structured habitat to the species. They tend to prefer rugged habitats and avoid plain terrain in Gobi. A model that assumes uniform space usage cannot incorporate this preference. Telemetry data indicates no effect of altitude in Gobi, which varies between 900 and 2100xx meters above MSL across the region. A recent publication (Johansson et al., 2016) from Tost reveals home range shapes that followed rugged mountain habitat. Our results reflect a similar pattern, with the spatial distribution of snow leopards’ ranging patterns being non-uniform with a preference for rugged terrain for the three study areas in South Gobi. The sign of a non-Euclidean beta parameter implies the covariate increases the “cost" of moving through regions with high covariate values, one can interpret this to be that this is a difficult kind of region to move through. In our case, when we look at the distances between recaptures for the animals, they tend to move short distances within the highly suitable habitats (the more rugged areas) and long distances when they cross from one suitable area to another. So in this case the low suitability regions are ones where animals move a long way through them and the high suitability regions are those where animals tend not to move far in them. This would manifest itself as highly suitable habitat being high “movement cost” regions and low suitability regions being a low “movement cost” regions. So by this argument, the positive sign of the Non-Euclidean beta parameter for Tost and Noyon corresponds to long movement distances tending to be through less suitable regions. This might be a result of animals hanging out it suitable regions most of the time, only occasionally “jumping” long distances between the highly suitable regions. If the suitable habitats were separated only by short regions of low suitability, rather than large tracts of highly suitable habitats, such as in case of Nemegt, our data generated a negative sign to the coefficient defining non-Euclidean distance metrics. In other words, the size and sign of coefficients of non-Euclidean distance metrics likely depends on the distribution of the covariate in the regions.

Field biologists also report preferences to certain micro-habitats by snow leopards for scraping and marking with urine (ref. xx), and these sites have been used for years to collect camera trapping and genetic data (e.g. ref. XX). Our camera trapping data also suggested possible affinity for micro-habitats. For instance sites with water-holes positively affected the expected encounter rate at distance zero from an activity centre (), especially during the summers in in Nemegt, a site that was sampled in summer. Topography influenced the expected encounter rate at distance zero from an activity centre ( in the model that compared all study areas (Table 2). Our results underscore that camera placement can have a strong effect on the detection functions.

Densities of snow leopards were found to vary within study areas as a function of habitat covariates. In our case, in South Gobi, terrain ruggedness defined spatial variation in density within study areas (Table 2). In other areas, similar modelling protocols can be used to understand more complex relationships such as variable prey densities, interaction with human and livestock, and effects of co-predators.

Several publications and reports recently have used posterior assessments of density surfaces (conditional probability density of activity centre locations, given the observed capture histories) based on camera trap locations (ref XX), generated by the software (or by using R functions such as fx.total) as maps of spatially-varying density. This is an incorrect interpretation and can be misleading. Even though it results in generation of surfaces that may appear to have density contours, these are not representative of the population (ref. XX). Our results reemphasize that these surfaces depend on the camera trap placements where the maps for the same study area may change if a different set of camera traps located differently are chosen for the same population. Density surfaces are best prepared using covariates in the analysis as opposed to the surfaces that are created using inbuilt functions that are strongly linked to the trap locations. With a uniform density model, for example, the conditional probability density will always be uniform far from the traps, and non-uniform near the traps, no matter how non-uniform the real activity centre distribution is far from the traps. More generally, with exactly the same actual locations of activity centres, but cameras placed in different locations, the expected value of the conditional probability density of activity centre locations would be different. The expected value of the conditional probability density of activity centres reflects the trap locations as much as it reflects the distribution of activity centres. Interpreting it to be reflecting only the distribution of activity centres is therefore incorrect and misleading. The conditional probability density of activity centre locations does not answer what we know about the relationship between density and spatial variables from a particular survey, but instead informs about what we know about the locations of individual activity centres from the survey. The survey always tells more about the locations of individuals close to the traps than those far away. Hence the conditional probability density surface always has more structure close to the traps than far away.

A wide range of conservation programs are being implemented at various scales across the snow leopard distribution range (ref. XX). Although the outputs and projected outcomes of these programs may vary, ultimately each of them aims at maintaining or improving snow leopard densities over the years (ref. XX). Moreover, the efficacy of different conservation models in the long-term can be tested by comparing trends in snow leopard densities (ref. XX). The ability to compare snow leopard densities and habitat use across space (different study areas) and time (different sessions in the same study area) has widespread conservation implications. In our case we found that the mean snow leopard density was marginally higher in the strictly protected study area and least in the unprotected study area. However, this was a function of extent of suitable habitat than conservation practice per se, where the proportion of suitable habitat per unit size of the study area was the maximum in case of Strictly Protected Area, followed by Partially Protected Area and unprotected area.

In addition to understanding ecological and conservation specific nuances of snow leopard abundance in comparing populations across space or time, we provide an application of the analytical framework to compare densities across multiple study areas that can also be used for monitoring populations across time. In our case, the density estimates did not vary between the three study areas, even though the effects of the various covariates differed. Our results highlight the importance of analysing biological 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.

Some recent studies have used spatial capture recapture for snow leopards (Alexander et al., 2016, Kumar XX), but the analyses have been limited to assume flat activity centre density models and patterns of space use that take no account of the habitat. Our results present a strong case that analyses of snow leopard populations using Spatial Capture Recapture should explore possible effects of covariates on density, detection function, and non-uniform distribution of activity patterns at the minimum. Absence of such analyses may result in spurious outcomes that can have strong biases (Sutherland et al., 2015). In our case, the results differed between 13xx%-30xx% between study areas. Failing to use covariates and non-Euclidean movement parameters in modelling snow leopard density seemingly biased the results for all the three study areas (Table 2), which is similar to the expected outcomes as reported by Sutherland et al (XX).

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 knowledge about the available tool-kits and lack of capacity have seemingly prevented their widespread use by ecologists. Through this paper, we analyse data from snow leopards representing three neighbouring habitats in South Gobi and investigate a series of models based on the species’ natural history and ecology, specifically the density, detection probability and movement patterns. We develop a range of candidate models, whose variants (depending on specific study areas) can be used to analyse data when reporting snow leopard populations from different study areas.

Table 1 Top 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: “stdBC” is a standardised binary variable for habitat suitability; “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; “sfac” is a factor variable indexing site; “noneuc” is described in Equations (4) to (6).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Site** | **Model** | **npar** | **logLik** | **AICc** | **dAICc** | **AICcwt** |
| Noyon | D~stdGC lambda0~1 sigma~1 noneuc~stdBC - 1 | 5 | -176.064 | 369.628 | 0 | 0.9515 |
| D~stdGC lambda0~Topo sigma~1 noneuc~stdGC - 1 | 7 | -172.364 | 377.395 | 7.767 | 0.0196 |
| D~stdGC lambda0~1 sigma~stdRgd | 5 | -180.354 | 378.207 | 8.579 | 0.013 |
| D~stdGC lambda0~1 sigma~1 noneuc~stdGC + stdBC - 1 | 6 | -177.457 | 378.915 | 9.287 | 0.0092 |
| Nemegt | D~stdGC lambda0~Water sigma~1 noneuc~stdGC - 1 | 6 | -95.8027 | 217.605 | 0 | 0.9933 |
| D~stdGC lambda0~1 sigma~1 noneuc~stdBC - 1 | 5 | -104.514 | 227.599 | 9.994 | 0.0067 |
| D~1 lambda0~1 sigma~1 noneuc~stdGC - 1 | 4 | -108.399 | 229.798 | 12.193 | 0 |
| Tost | D~stdGC lambda0~1 sigma~1 noneuc~stdBC - 1 | 5 | -200.298 | 418.095 | 0 | 0.9879 |
| D~stdGC lambda0~Water sigma~1 noneuc~stdGC - 1 | 6 | -201.45 | 426.9 | 8.805 | 0.0121 |
| D~1 lambda0~1 sigma~1 | 3 | -210.307 | 429.014 | 10.919 | 0 |
| All together | D~stdGC lambda0~Topo sigma~1 noneuc~stdGC - 1 | 7 | -498.062 | 1013.324 | 0 | 1 |
| D~stdGC \* sfac lambda0~Topo sigma~1 noneuc~stdGC - 1 | 11 | -496.447 | 1023.41 | 10.086 | 0 |

Table 2 Coefficients of parameters and estimates of snow leopard abundance from the three study areas, based on most parsimonious 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.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Site | Parameter | Top model Coefficient | LCL | UCL | Top model Abundance (95% CI) | Null model Abundance (95% CI) |
| Nemegt | (*D*) | -9.29 | -10.09 | -8.48 | 20.01  (14.57-44.20) | 15.16  (13.48-22.75) |
| (*D*) | 0.1 | -0.81 | 1.00 |
|  | -4.19 | -4.68 | -3.71 |
|  | 2.06 | 1.33 | 2.79 |
| () | 8.27 | 7.71 | 8.83 |
| (noneuc) | -0.37 | -0.73 | -0.01 |
| Noyon | (*D*) | -11.30 | -12.68 | -9.91 | 14.58  (14.07-18.59) | 15.85  (14.40-22.59) |
| (*D*) | 1.37 | 0.86 | 1.87 |
| () | -3.70 | -4.12 | -3.29 |
| () | 8.86 | 8.72 | 8.99 |
| (noneuc) | 1.09 | 0.91 | 1.27 |
| Tost | (*D*) | -10.45 | -11.42 | -9.47 | 14.20  (14.01-16.88) | 15.69  (14.35-22.22) |
| (*D*) | 1.02 | 0.62 |  |
| () | -3.82 | -4.20 | -3.44 |
| () | 8.68 | 8.54 | 8.83 |
| (noneuc) | 1.11 | 0.88 | 1.35 |

Figure 1: Study Area and Snow Leopard Distribution (inset)

Figure 2a: Visual depiction of least cost paths between random points in the Tost study area (from green to red dots) defined by terrain ruggedness index



Figure 2b: Visual depiction of probabilities of getting to arbitrarily selected locations (black dots in white circles) from anywhere using the estimated least-cost path distance metric defined by terrain ruggedness in the Tost study area



Figure 4a: Snow leopard density surface generated based on the most parsimonious models

Figure 4b: Snow leopard surface generated using posterior estimates of individuals’ locations