**Stuff that you've been missing: Improving ecological inferences about snow leopard populations from Spatial Capture Recapture Analysis**

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**Abstract**

(to come…)

**Introduction**

Less than 1.5% of the global snow leopard range has ever been sampled using systematic camera trapping 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 availability of digital camera traps has made it possible to sample snow leopards using camera traps across study areas large enough for the purpose of estimating and monitoring populations (Sharma et al., 2014). Few studies have been conducted at scales that can be used to infer snow leopard population sizes or population dynamics without risking misinterpretations caused by small sampling areas (Sharma et al., 2014). Even then, most studies have used conventional capture recapture analyses that require inadequate or ad hoc estimation of effective sampling area and hence may lead to inaccurate density estimates (ref. XX).

Spatial Capture Recapture (SCR) methods to estimate wildlife population density and size in a spatially distributed population were first introduced by Efford (2004), and have developed rapidly since. Royle et al. (2013) give a detailed review and introduction to SCR methods, while Borchers and Fewster, (2016) provide a synthesis and overview of the field as at 2016 as well as speculations on future developments. Two developments that are important for analysis of snow leopards data are (1) methods for modelling non-uniform activity centre density (Borchers and Efford, 2008) and (2) methods for modelling non-uniform space usage, via of non-Euclidian distance metrics (J. Andrew Royle et al., 2013; Sutherland et al., 2015). Non-Euclidian distance metrics allow the capture probability to depend on the habitat that individuals need to move through to encounter camera traps, and so model habitat-dependent space use around activity centres. 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.

Some publications and reports also present posterior estimates of individuals’ locations as if they are activity centre density surfaces (Alexander et al., 2016; Thinley et al., 2016). This is an incorrect and misleading interpretation. These are not density surfaces. They will always show most contrast close to detectors, whether or not that is where most variation in density occurs, and will be systematically different (as opposed to random fluctuation) for different detector locations, even when exactly the same individuals are being surveyed. <See Appendix, if David can get it done in time.>

Snow leopards are known to have large home ranges of the order of 250-700 sq km in size (Johansson et al., 2016). 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 addition, because snow leopard distribution is closely aligned to habitat types and demonstrates strong spatial preferences, and individual home ranges tend to be larger than the length or width of individual habitat patches (Johansson et al., 2016), inferences assuming ranging patterns around an activity centres that take no account of habitat types could lead to biases.

We analyse three neighbouring snow leopard populations in South Gobi, Mongolia to explore the effects of habitat covariates on detection probability, density and ranging patterns. 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. We also compare the densities between the three study areas using information theoretic approach. The results provide a set of general guidelines for the analysis of snow leopard populations in mountain habitats.

**Methodology**

***Study Area***

South Gobi is an important snow leopard habitat (fig 1XX, 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, even though the livestock population is rather high with a density of XX heads per sq km. In 2008, the first ever long-term snow leopard research was initiated in the Tost-Tosonbumba Mountains of South Gobi. These mountains are partially protected through community based conservation programs such as Snow Leopard Enterprise and Livestock Insurance programs operational since 19XX and 2009 respectively (ref. XX). Recently though, the mountain range has been encompassed in a Protected Area by the Government of Mongolia. 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 at least XX operational mines extracting coal and XX, Nemegt Mountains represent the strictly Protected Area of Gurvan Saikhan National Park. The three Mountain ranges are separated by several kilometres of steppe (fig XX). 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 popualtions. The number of cameras varied between 30 and 40, depending on the minimum convex polygon of the sampled area 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, 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 (SE11.81), 50.47 (SE4.44) and 89.89 (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.

**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). 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 with 1 representing snow leopard habitat and 0 denoting non-habitat. We identified contiguous habitats defined by high terrain ruggedness index and created polygons that defined habitats as 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. Terrain Ruggedness Index was generalized 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 influencing density.

***Data preparation***

We obtained 108, 54 and 93 snow leopard encounters respectively on camera traps (fig xx, camera trap layout) from partially protected, strictly protected and unprotected sampling areas. 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 waterhole within 50m from the camera traps. 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 were able to consider the entire sampling as a single occasion and session. This allowed for faster analysis across large spatial extents for the three study areas. All but binary covariates data were standardized for ease of comparison between models.

***Data analysis***

We used the R package secr (Efford, 2016) to develop population models for the three sampled areas using Maximum Likelihood (frequentist) approach. Candidate model sets were developed for each sampled area separately to investigate for each area the effect of various hypotheses that identify with snow leopard behaviour, ecology and natural history.

The probability of capturing snow leopards, given presence is likely to be affected by the topography of the sites where the camera traps are installed. Similarly, they are likely to be attracted to waterholes. We investigated the effect of terrain ruggedness, topography and presence of waterholes.

Telemetry data from 20 snow leopards report that snow leopards show strong selection of rugged habitat types and avoid flat habitats for their routine movements within the maximum convex polygons of their home ranges. Models assuming non-uniform ranging patterns around activity centres of the snow leopards using non-Euclidean distance metrics as a function of habitat were compared with those considering activity patterns that depend only on Euclidean distance from activity centres. This was done using least cost path analysis where the cost of moving from one point to the other was estimated as a function of terrain ruggedness.

Conventional population analyses assume uniform density across the study areas and provide no option to incorporate spatial variation in densities at resolutions finer than whole strata. However, recent developments in SECR methods allow estimation of density as a function of ecologically meaningful covariates. We investigated if snow leopard densities were dependent on terrain ruggedness and estimated a non-uniform density surface for each study area. We compare these with maps generated by using posterior estimates of individuals’ locations, where the latter is often misinterpreted as a density surface.

Lastly, we also fitted models to all three areas simultaneously and used AICc to select between models and investigate whether effects were area-specific or shared across areas. We used this analysis to compare densities in the strictly protected, partially protected and unprotected areas.

**Results**

The best models by AIC were found to differ between the three study areas. However, habitat dependent, non-Euclidean space use with density dependent on habitat quality, here defined by terrain ruggedness index, were the top models in case of each study area. The habitat-dependent space use models are based on non-Euclidian least cost path distances (Royle et al., 2013; Sutherland et al., 2015). Having fitted such a model 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 prior to analysis as ``bridges’’ between the high-usage habitats – because of intervening ``islands’’ of good habitat (see Figure XX, for example). On the basis of habitat covariates, 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. This matched more than 35,000 GPS locations from 20 snow leopards, and explained the non-Euclidean ranging patterns of the snow leopards around their activity centres (Figure XX).

Density estimates too varied with habitat each of the three study areas. The probability of detection at trap locations was affected by topography and water in two study areas. Both topography and presence of waterholes affected the expected encounter rate at distance zero from an activity centre (parameter ) in case of strictly protected and partially protected study areas.

Our estimated conditional probability density function of activity centre locations and our estimated density surface produced starkly different maps. The latter is a valid representation of activity centre distribution, whereas the former is not.

Remarkably, population estimates for the most parsimonious models differed between 10% and 28% when compared with the estimates from the null models that consider flat density, no effect of covariates on detection probability and Euclidean ranging patterns. Failing to use covariates and non-Euclidean movement parameters in modelling snow leopard density biased the results positively for the partially and strictly protected study area, whereas the bias was negative for the unprotected study area.

Mean snow leopard densities ranged between 0.75 per 100 km2 in the strictly protected (95% CI = 0.71-0.97) and unprotected (95% CI = 0.72-0.89) areas, and 1.12 (95% CI = 1.05-1.31) per 100 km2 in the partially protected study area. The best model selected based on AICc indicated that ruggedness affected density differently between the three study areas, and that presence of waterholes also had different effects on each of the three study areas. Incidentally, animals in Noyon, which was sampled during the winter, showed no significant affinity for waterholes.

**Discussion**

Snow leopard are a habitat specialist and mountain ranges such as the ones in South Gobi provide a highly structured habitat to the species. As a result, a model that assumes uniform space usage cannot model this preference. Telemetry data indicates no effect of altitude in Gobi, which varies between 900 and 2100xx meters above MSL. A recent publication (Johansson et al., 2016) from Tost (partially protected) reveal 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.

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 sites with water-holes, especially during the summers. In our case in Gobi, we found strong support for models that used a binary variable for presence of water, and topography as the two covariates influencing the expected encounter rate at distance zero from an activity centre (. Our results underscore that camera placement has a strong effect on the detection functions, primarily on rather than the range parameter () in our case. Coefficients from the study area that was sampled during winter show negligible effect of waterholes on detection probability, which can be explained by the availability of snow throughout the study area.

Densities of snow leopards were found to vary within study areas as a function of habitat covariates. In our case, in South Gobi, it was the terrain ruggedness that defined spatial variation in density within and across study areas. However in other areas, similar 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 fancy looking surfaces, 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 as if it reflected only the distribution of activity centres is therefore incorrect and misleading. The conditional probability density of activity centre locations does not address the question “What do I know about the relationship between density and spatial variables from this survey?”, it answers the question “What do I know about the locations of individual activity centres from this 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.

Several 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 they are aimed at maintaining or improving snow leopard densities over the years (ref. XX). Similarly, the efficacy of different conservation models in the long-term can be tested most effectively by comparing 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. We provide an application of the analytical framework to compare densities across three different study areas that can also be used for monitoring populations across time. In our case, not only did the density estimates vary between the three study areas, so did the effect of the various covariates. 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.

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 positive as well as negative biases (Sutherland et al., 2015). In our case, there were differences of nearly 13% in one area, and up to XX and 30% in the other two study areas.

Although new, 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 understanding of 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. We developed a range of candidate models, whose variants (depending on specific study areas) should be analysed when reporting snow leopard populations from different study areas. We also provide the modelling approach to compare densities and effects of various covariates on density, detection probability and movement patterns.

Table XX: Candidate model sets from the three study areas, corresponding AICc and AICc weights (stdGC =

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Area | Model | npar | logLik | AICc | dAICc | AICcwt |
| Nemegt | D~stdGC lambda0~Water sigma~1 noneuc~stdGC – 1 | 6 | -137.033 | 296.566 | 0 | 0.974 |
|  | D~stdGC lambda0~Topo + Water sigma~1 noneuc~stdGC – 1 | 7 | -136.905 | 303.811 | 7.245 | 0.026 |
|  | D~1 lambda0~1 sigma~1 | 3 | -150.231 | 308.644 | 12.078 | 0 |
|  | D~1 lambda0~1 sigma~1 noneuc~stdGC – 1 | 4 | -149.035 | 310.07 | 13.504 | 0 |
|  | D~stdGC lambda0~1 sigma~1 | 4 | -150.105 | 312.209 | 15.643 | 0 |
|  | D~stdGC lambda0~1 sigma~1 noneuc~stdBC – 1 | 5 | -148.498 | 313.663 | 17.097 | 0 |
|  | D~stdGC lambda0~1 sigma~1 noneuc~stdGC - 1 | 5 | -149.004 | 314.675 | 18.109 | 0 |
|  | D~1 lambda0~stdRgd sigma~stdRgd | 5 | -149.606 | 315.878 | 19.312 | 0 |
|  | D~stdGC lambda0~stdRgd sigma~1 | 5 | -149.704 | 316.074 | 19.508 | 0 |
|  | D~stdGC lambda0~1 sigma~stdRgd | 5 | -150.037 | 316.742 | 20.176 | 0 |
|  | D~stdGC lambda0~Topo sigma~1 noneuc~stdGC - 1 | 6 | -147.133 | 316.765 | 20.199 | 0 |
|  | D~stdGC lambda0~1 sigma~1 noneuc~stdGC + stdBC - 1 | 6 | -148.392 | 319.285 | 22.719 | 0 |
| Noyon | D~stdGC lambda0~1 sigma~1 noneuc~stdBC - 1 | 5 | -212.795 | 443.091 | 0 | 0.4385 |
|  | D~stdGC lambda0~1 sigma~1 noneuc~stdGC + stdBC - 1 | 6 | -209.968 | 443.936 | 0.845 | 0.2874 |
|  | D~stdGC lambda0~1 sigma~1 noneuc~stdGC - 1 | 5 | -213.376 | 444.253 | 1.162 | 0.2453 |
|  | D~stdGC lambda0~Topo sigma~1 noneuc~stdGC - 1 | 6 | -212.918 | 449.835 | 6.744 | 0.0151 |
|  | D~stdGC lambda0~Water sigma~1 noneuc~stdGC - 1 | 6 | -213.013 | 450.026 | 6.935 | 0.0137 |
|  | D~stdGC lambda0~Water + Topo sigma~1 noneuc~stdGC - 1 | 7 | -212.789 | 458.245 | 15.154 | 0 |
|  | D~1 lambda0~1 sigma~1 | 3 | -225.693 | 459.787 | 16.696 | 0 |
|  | D~1 lambda0~1 sigma~1 noneuc~stdGC - 1 | 4 | -224.496 | 461.437 | 18.346 | 0 |
|  | D~stdGC lambda0~1 sigma~stdRgd | 5 | -222.209 | 461.917 | 18.826 | 0 |
|  | D~1 lambda0~Topo sigma~1 | 4 | -225.386 | 463.216 | 20.125 | 0 |
|  | D~1 lambda0~stdRgd sigma~stdRgd | 5 | -222.873 | 463.247 | 20.156 | 0 |
|  | D~stdGC lambda0~1 sigma~1 | 4 | -225.571 | 463.586 | 20.495 | 0 |
|  | D~1 lambda0~Water sigma~1 | 4 | -225.689 | 463.822 | 20.731 | 0 |
|  | D~1 lambda0~Topo + Water sigma~1 | 5 | -225.36 | 468.22 | 25.129 | 0 |
| Tost | D~stdGC lambda0~Topo sigma~1 noneuc~stdGC - 1 | 6 | -226.801 | 471.603 | 0 | 0.3643 |
|  | D~stdGC lambda0~1 sigma~1 noneuc~stdGC + stdBC - 1 | 6 | -227.218 | 472.435 | 0.832 | 0.2403 |
|  | D~stdGC lambda0~Water sigma~1 noneuc~stdGC - 1 | 6 | -227.305 | 472.61 | 1.007 | 0.2202 |
|  | D~stdGC lambda0~1 sigma~1 noneuc~stdBC - 1 | 5 | -229.769 | 473.537 | 1.934 | 0.1385 |
|  | D~stdGC lambda0~Topo + Water sigma~1 noneuc~stdGC - 1 | 7 | -226.791 | 476.197 | 4.594 | 0.0366 |
|  | D~1 lambda0~1 sigma~1 noneuc~stdGC - 1 | 4 | -243.644 | 497.788 | 26.185 | 0 |
|  | D~stdGC lambda0~1 sigma~1 noneuc~stdGC - 1 | 5 | -248.124 | 510.248 | 38.645 | 0 |
|  | D~1 lambda0~1 sigma~1 | 3 | -252.943 | 513.297 | 41.694 | 0 |
|  | D~1 lambda0~Topo sigma~1 | 4 | -251.727 | 513.955 | 42.352 | 0 |
|  | D~1 lambda0~Water sigma~1 | 4 | -252.13 | 514.76 | 43.157 | 0 |
|  | D~stdGC lambda0~1 sigma~1 | 4 | -252.663 | 515.826 | 44.223 | 0 |
| Together | D~stdGC \* sfac lambda0~Water \* sfac sigma~1 noneuc~stdGC - 1 | 14 | -531.883 | 1102.536 | 0 | 0.9915 |
|  | D~stdGC \* sfac lambda0~(Water + Topo) \* sfac sigma~1 noneuc~stdGC - 1 | 17 | -530.527 | 1112.053 | 9.517 | 0.0085 |
|  | D~stdGC lambda0~Water sigma~1 | 5 | -576.453 | 1164.157 | 61.621 | 0 |
|  | D~stdGC \* sfac lambda0~Water sigma~1 noneuc~stdGC - 1 | 10 | -570.246 | 1165.609 | 63.073 | 0 |
|  | D~stdGC lambda0~Topo sigma~1 | 5 | -578.206 | 1167.663 | 65.127 | 0 |
|  | D~stdGC lambda0~1 sigma~1 noneuc~stdGC - 1 | 5 | -579.519 | 1170.288 | 67.752 | 0 |
|  | D~stdGC lambda0~Topo + Water sigma~1 | 6 | -579.688 | 1173.163 | 70.627 | 0 |
|  | D~1 lambda0~1 sigma~1 noneuc~stdGC – 1 | 4 | -582.65 | 1174.116 | 71.58 | 0 |
|  | D~stdGC + sfac lambda0~1 sigma~1 noneuc~stdGC – 1 | 7 | -579.286 | 1175.008 | 72.472 | 0 |
|  | D~stdGC lambda0~1 sigma~Topo | 5 | -583.167 | 1177.585 | 75.049 | 0 |
|  | D~stdGC \* sfac lambda0~1 sigma~1 noneuc~stdGC – 1 | 9 | -577.77 | 1177.631 | 75.095 | 0 |
|  | D~1 lambda0~1 sigma~1 | 3 | -590.588 | 1187.656 | 85.12 | 0 |
|  | D~stdGC lambda0~1 sigma~1 | 4 | -589.969 | 1188.753 | 86.217 | 0 |

Table XX (maybe in an appendix?): Estimated parameters Estimates of snow leopard density and abundance from the preferred three study areas, based on most parsimonious and the base-models.

Table XX: Coefficients!

Figure XX: Visual depiction of least cost paths between random points(David to provide from his talks!)

Figure XXb: Visual depiction of non-Euclidean ranging patterns around randomly chosen sampling locationxx

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

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