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

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**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 ad hoc estimation of effective sampling area and hence may lead to inaccurate density estimates.

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)( Borchers et al., 20XX) 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)xxKumarxx, 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 recent publications 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 three 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 and result in biased 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 spurious inferences.

We analyse three neighbouring snow leopard populations in South Gobi, Mongolia to explore the effects of habitat covariates on detection function, 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. 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. 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 few 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 and removal date was recorded 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). 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, we developed 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 15xx 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 for more than 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 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 from partially protected, strictly protected and unprotected sampling areas. Each encounter was identified into individuals 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, accurately up to 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, and hence 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.

***Data analysis***

We used the R package secr (Efford, 2016) to develop population models for the three sampled areas. Candidate model sets were developed for each sampled area to test 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 tested 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-Euclidean ranging patterns around activity centres of the snow leopards were compared with those considering Euclidean activity patterns. 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 analyses assume uniform density across the study areas. However, methods in SECR allow estimation of density as a function of ecologically meaningful covariates. We tested if snow leopard densities were non-uniform as function of terrain ruggedness and generated a non-uniform density surface for each study area. We compare these with maps generated by using posterior estimates of individuals’ locations.

Lastly, we tested whether densities in the strictly protected, partially protected and unprotected areas differed from each other. Since the three study areas reported different effects of covariates, we also tested for the possibility of an interaction between the study areas and the covariates.

**Results**

Model inference with the most parsimonious models varied across the three study areas. However, 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. Least cost path analysis between different points identified patterns of connectivity between habitat patches, and identified bridges that the animals may have used while avoiding less suitable habitats. 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. Probability of detection at trap locations was affected by topography and water in two study areas each. Both topography and presence of waterholes affected lambda in case of strictly protected and partially protected study areas.

Comparison the summed probability density functions of home-range centre probability functions and density surface as a function of a particular covariate produced starkly different maps, thus underscoring why the results generated from posterior estimates of individuals’ locations should be used with caution.

Remarkably, population estimates for the most pa

rsimonious models were biased between 10% and 28% when compared with the estimates from the null models. 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.

Snow leopard densities were similar/different<<xx yet to run the final model with all covariates. Codes are ready>> when we compared them across the three sampled areas.

Table XX: Candidate model sets from the three study areas, corresponding AICc and AIC weights, and estimates of snow leopard density and abundance.

Figure XX: Visual depiction of least cost paths between random points,

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

Figure XXa: Snow leopard density surface generated based on the most parsimonious model

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

**Discussion**

1. All snow leopard data shows non-Euclidean distribution of sigma (habitat use is essentially non-Euclidean)
2. Model based inferences without consideration of non-euclidean estimation of sigma and effect of covariates on density, detectability and activity patterns tend to bias the population estimates, sometimes up to 30%.
3. Density between the three sampling areas was/was not significantly different, XX. Explain the patterns
4. Snow leopard are a habitat specialist and mountain ranges such as the ones in South Gobi provide a structured habitat to the species, that  prevents uniform usage as expected by Euclidean analysis of home ranges.
5. 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-Euclidean distribution of activity patterns at the minimum.
6. Absence of such analyses may result in spurious outcomes that can have strong positive as well as negative biases XX.
7. 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.

**References**

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