

ORIGINAL ARTICLE

Sampling bias in snow leopard population estimation studies

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Abstract

Accurate assessments of the status of threatened species and their conservation planning require reliable estimation of their global populations and robust monitoring of local population trends. We assessed the adequacy and suitability of studies in reliably estimating the global snow leopard (*Panthera uncia*) population. We compiled a dataset of all the peer-reviewed published literature on snow leopard population estimation. Metadata analysis showed estimates of snow leopard density to be a negative exponential function of area, suggesting that study areas have generally been too small for accurate density estimation, and sampling has often been biased towards the best habitats. Published studies are restricted to six of the 12 range countries, covering only 0.3–0.9% of the presumed global range of the species. Re-sampling of camera trap data from a relatively large study site (c.1684 km²) showed that small-sized study areas together with a bias towards good quality habitats in existing studies may have overestimated densities by up to five times. We conclude that current information is biased and inadequate for generating a reliable global population estimate of snow leopards. To develop a rigorous and useful baseline and to avoid pitfalls, there is an urgent need for (a) refinement of sampling and analytical protocols for population estimation of snow leopards (b) agreement and coordinated use of standardized sampling protocols amongst researchers and governments across the range, and (c) sampling larger and under-represented areas of the snow leopard's global range.

KEYWORDS

camera trap, Central Asia, Himalaya, meta-analysis, monitoring, *Panthera uncia*, population ecology

1 | INTRODUCTION

Robust information on the distribution and population trends of threatened species is important for effective conservation planning. Understanding the distribution range helps in directing conservation efforts to areas where they are most needed or efficiently implemented. Monitoring trends in population helps assess species status and the impact of conservation efforts. For instance, the International Union for Conservation of Nature (IUCN) Red list of Threatened Species—a widely recognized global platform for evaluating

the conservation status of species—uses information on distribution, global population and population trends for Red List designation (IUCN, 2018). Thus, the accuracy of information on distribution and population trends is crucial for robust conservation status assessments. However, reliable population information can be hard to obtain for carnivores because they often occur at low densities, are nocturnal, elusive and range over relatively large areas (Alibhai, Jewell, & Evans, 2017; Karanth, Nichols, Kumar, Link, & Hines, 2004). Over the past two decades, technological developments with camera traps and molecular genetics have

improved our ability to estimate the density and abundance of large carnivores (Burton et al., 2015; Karanth, 1995; Maffei, Noss, Cuellar, & Rumiz, 2005). Several statistical tools have also been developed to analyse population data with imperfect detections (Francis, Barker, & Cooch, 2014).

Snow leopards *Panthera uncia* (Felidae) occur in the mountainous regions of 12 countries of central and south Asia. They are a flagship species for the conservation of Asia's high-altitude ecosystems, which are also considered to be the water towers of the continent. The species faces numerous threats including depletion of its wild herbivore prey, habitat destruction by large infrastructure projects and mining, poaching, and persecution over its livestock predation behaviour (Mishra et al., 2003; Snow Leopard Network, 2014; Suryawanshi, Bhatnagar, Redpath, & Mishra, 2013). There is widespread acceptance that snow leopard conservation efforts need to go beyond protected areas (PAs) and impact large landscapes to secure their populations (Johansson et al., 2016; Mishra et al., 2018; Snow Leopard Working Secretariat, 2013).

The estimates proposed for the global snow leopard population in literature vary from a low of 3,920 (Snow Leopard Working Secretariat, 2013) to a high of 8,745 (McCarthy, Mallon, Sanderson, Zahler, & Fisher, 2016). These estimates are based largely on expert opinion, interviews, questionnaire surveys and counting snow leopard signs—techniques that do not yield scientifically robust estimates. For example, the estimate by McCarthy et al. (2016) are based on interview surveys (35 sites), expert opinions (11 sites) and sign surveys (36 sites), and other research such as telemetry and livestock attacks (9 sites), while the use of scientifically acceptable camera trap data (5 sites) was limited. Interview surveys, expert opinions and livestock attacks are useful for presence and distribution surveys, but unreliable for estimating populations (Jones, Adriamarovololona, Hockley, Gibbons, & Milner-Gulland, 2008). Similarly, estimates of the size of the global snow leopard distribution range vary from 1,230,000 (Fox, 1989) to 3,024,728 km² (Hunter & Jackson, 1997), and rely more on expert opinion and relatively crude geo-spatial modelling than on empirical presence-absence data.

The only robust sources of information on snow leopard population sizes come from studies that use sample counts based on camera trap (Karanth & Nichols, 1998) or molecular genetics (Mondal et al., 2009) and model for imperfect detection. A standard camera trap based estimation involves setting up remote sensor cameras in the area of interest. The cameras are placed in the micro-habitats that are preferred by snow leopards but spread across the study area in a uniform grid system or distributed randomly in space (Alexander, Gopalaswamy, Shi, & Riordan, 2015; Jackson, Roe, Wangchuk, & Hunter, 2006; O'Connell, Nichols, & Karanth, 2010; Sharma et al., 2014). Individual snow leopards are identified from photographs using individually

distinct spot patterns on the fur and the data are analysed using individual capture histories to estimate abundance and area sampled (Alexander et al., 2015; Sharma et al., 2014). The method assumes that individual snow leopards can be identified accurately from camera trap photographs, though this assumption has not been tested. Similarly, samples of snow leopard faeces can be collected from the area of interest with relatively uniform spatial coverage across the study area. Individual snow leopards are then identified by extracting and analysing DNA from these samples and the data are similarly modelled in a capture recapture framework to estimate the abundance of snow leopards in the area sampled (Janečka et al., 2008; Mondal et al., 2009; Suryawanshi et al., 2017). Both these methods have become popular especially following their widespread adoption in monitoring tiger (*Panthera tigris*) populations (Karanth et al., 2004; Karanth & Nichols, 1998). Over the last decade, several such studies of snow leopard population estimation have been conducted in different parts of Asia (Table 1).

In this paper, we review all the published, peer-reviewed studies on snow leopard population estimation that have employed the scientifically acceptable methods of camera trapping and faecal genetics. We aimed to examine their suitability and adequacy in arriving at a reliable estimate of the global snow leopard population. We compiled a dataset (Table 1) and to ensure data and information quality, we restricted our study to peer reviewed publications. We examined the spatial extent and distribution of these studies to assess their geographical representativeness. Because snow leopards are wide ranging species with large home ranges (average annual home range 207 km² ± 63 SD for males and 124 km² ± 41 SD for females with low home range overlap; Johansson et al., 2016), we also examined the size distribution of study areas to assess if they were large and representative enough to derive reliable density estimates for their respective landscapes.

Our findings highlight the inadequacy of currently available information for global snow leopard population estimation. We underscore the need for extensive collaboration amongst researchers and governments in developing and employing standardized sampling protocols and undertaking snow leopard population assessments in an appropriately stratified and randomized manner.

2 | METHODS

2.1 | Literature review

We compiled all the published studies on population estimation of snow leopards from international peer-reviewed journals (see Table 1 & Figure 1). For each study we recorded information on: Location (country and region), duration (year, start and end dates), survey methods (e.g., camera trapping or genetic analysis), effectively sampled area

TABLE 1 Table representing all the peer-reviewed studies on snow leopard population estimation

Study (no. of estimates)	Site	Country	Eff. Sam. Area (km ²)	PA	Year	Abundance	Density (/100km ²)	Sampling method	Method abundance	Method density
Jackson et al., 2006	Hemis	India	135	1	2004	6	4.45	CT	CCR	Half MMDM
Ditto	Hemis	India	71	1	2003	6	8.49	CT	CCR	Half MMDM
McCarthy et al., 2008 (6)	Sarychat	Kyrgyzstan	655	1	2005	1	0.15	CT	CCR	HRB
Ditto	Sarychat	Kyrgyzstan	655	1	2005	3	0.46	GA	TC	CE
Ditto	Jangart	Kyrgyzstan	808	0	2005	7	0.87	CT	CCR	HRB
Ditto	Jangart	Kyrgyzstan	808	0	2005	5	0.62	GA	TC	CE
Ditto	Tomur	China	813	1	2005	6	0.74	CT	CCR	HRB
Ditto	Tomur	China	813	1	2005	9	1.11	GA	TC	CE
Jackson, Munkhtsog, Mallon, Naranbaatar, & Gerelmaa, 2009 (1)	Tost Uul	Mongolia	264	0	2007	4	1.52	CT	CCR	Half MMDM
Lovari et al., 2009 (1) ^a	Sagarmatha	Nepal	571	1	2005–2006	4	0.70	GA	TC	CE
McCarthy, Murray, Sharma, & Johansson, 2010 (1)	Tost Uul	Mongolia	1,300	0	2009	10	0.77	CT	CCR	CE
Janečka et al., 2011 (4) ^b	Noyon Uul	Mongolia	155.5	0	2007	6	3.86	GA	TC	CE
Ditto	Tost Uul B	Mongolia	59.8	0	2007	4	6.68	GA	TC	CE
Ditto	Tost Uul A	Mongolia	108	0	2007	5	4.63	GA	TC	CE
Wegge, Shrestha, & Flagstad, 2012 (1)	Phu Valley	Nepal	95	1	NA	6	6.32	GA	TC	CE
Sharma et al., 2014 (3)	Tost Uul	Mongolia	1,680	1	2010	14	0.83	CT	CCR	CE
Ditto	Tost Uul	Mongolia	1,680	1	2011	12	0.71	CT	CCR	CE
Ditto	Tost Uul	Mongolia	1,680	1	2012	14	0.83	CT	CCR	CE
Alexander et al., 2015 (1)	Qilianshan	China	480	1	2013	20	3.31	CT	Bayesian SECR	Bayesian SECR
Alexander, Zhang, Shi, & Riordan, 2016 (1)	Qilianshan	China	375	1	2013–2014	17–19	1.40	CT	Bayesian SECR	Bayesian SECR
Guoliang et al., 2016 ^c	Bortala	China	192	0	2012–2013	11–15	5.73–7.81	CT	NA	CE
Chen et al., 2017 (1) ^d	Qoumulungma	China	326	1	2014	7	1.8–2.5	CT	NA	CE
Kachel, McCarthy, McCarthy, & Oshurmamadov, 2017 (2)	Madiyan	Tajikistan	1,000	0	2012	6	0.46	CT	ML SECR	ML SECR
Ditto	Murghab	Tajikistan	1,000	0	2012	14	0.74	CT	ML SECR	ML SECR
Suryawanshi et al., 2017 (7)	Lingti	India	240	1	2010	8	3.33	GA	CCR	CE
Ditto	Lossar	India	219	0	2010	1	0.46	GA	CCR	CE
Ditto	Kibber	India	411	1	2010	8	1.95	GA	CCR	CE
Ditto	Pin	India	270	1	2010	2	0.74	GA	CCR	CE
Ditto	Tabo	India	341	0	2010	4	1.17	GA	CCR	CE
Ditto	Rumtse	India	300	0	2011	5	1.67	GA	CCR	CE
Ditto	Tost Uul	Mongolia	250	0	2011	5	2	CT	CCR	CE

Note. A “Study” is defined by a peer-reviewed article. A “Site” is study area for which the population estimation was being conducted. “Year” is the year when the study was conducted. “Eff. Sam. Area” is the effective sampled area to which the densities are extrapolated. “Sampling Method” is the field method used to obtain population estimates, “CT” = Camera trapping and “GA” Genetic Analysis. “Abundance” is number of individual snow leopards reported at each site. “PA” refers to protected area, wherein “1” = Protected Area and “0” = Non-Protected Area. For “Method Abundance”, “CCR” = Closed Capture-Recapture, “TC” = Total Count and “ML SECR” = Maximum Likelihood SECR. For “Method Density” is the analytical method used for density estimation, “CE” = Crude Estimate, “HRB” = Home Range Buffer, “Half MMDM” = Half Mean Maximum Distance Moved and “ML SECR” = Maximum Likelihood SECR.

^a Lovari et al., 2009: There is no mention of study area size in the paper. The density estimate for snow leopard is quoted in individuals 1,000 km⁻² (7 individuals/1000km²). To calculate study area we first converted the density to /100km² (reported in table) as is conventionally reported for snow leopards and using the information that 4 individuals were found in study area, we used simple ratios to calculate study area.

^b Janečka et al., 2011: This paper also reports a camera trap density of snow leopard from Tost Uul. This estimates is from the study conducted and represented in Jackson et al., 2009 (see table) hence we don't include it under this study as well.

^c Guoliang et al., 2016: As the estimated densities is a range of values, we used the mean value (6.75 individuals 100 km⁻²).

^d Chen et al., 2017: There is no mention of the exact study area size and the density estimate for snow leopard is given as a range (see table). We calculate the study area size using the mean density of snow leopard individuals 100 km⁻² (2.15). Like Guoliang et al., 2016 this mean density (2.15 individuals/ 100km²) was used for analysis.

(unless explicitly stated otherwise, the sampled area was taken to be the effectively sampled area), minimum number (abundance) of snow leopards identified, reported estimates

of snow leopard abundance and estimation method (e.g., closed capture–recapture), density of snow leopards and estimation method (e.g., spatially explicit capture–

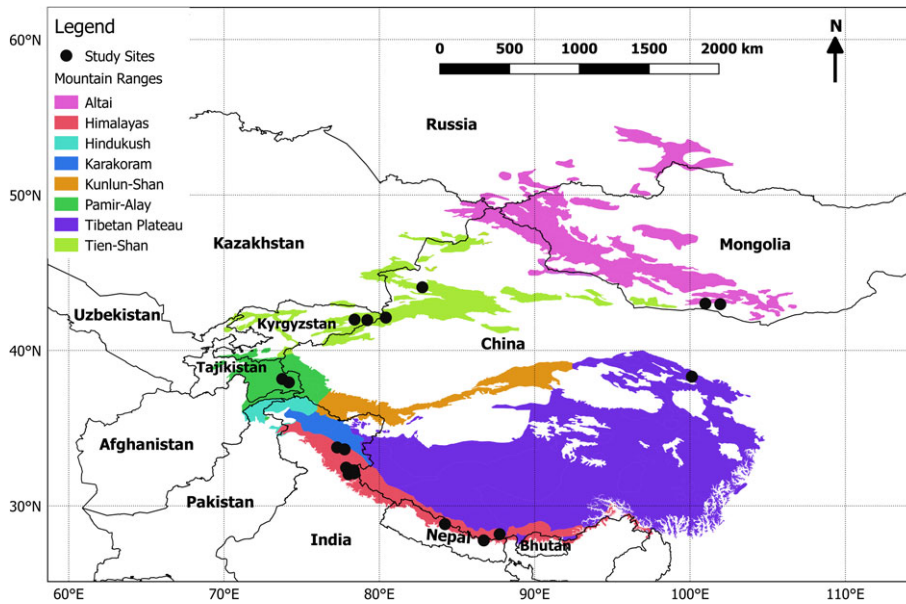


FIGURE 1 Sites where snow leopard population estimation exercises have been conducted using camera traps or genetics, and reported in peer-reviewed scientific literature. The coloured region shows the presumed global snow leopard distribution, with different colours depicting each of the major mountain chains

recapture [SECR], Half Mean Maximum Distance Moved [MMDM]), and whether the study was conducted in a PA or outside. Where appropriate, we recorded additional remarks to better describe the study (e.g., “Density not estimated”). For studies that did not report densities but had estimated abundance, we calculated a crude density estimate by dividing the estimated abundance with the effectively sampled area (as reported in the study). We plotted all study area locations over the presumed global distributional range of snow leopards, and highlighted the rough boundaries of each of Asia’s major mountain chains. Here we treat each estimate as an independent data point. While multi-year estimates from the same site may not be completely independent, we had to treat them as independent given the limited amount of published estimates of snow leopard populations. We had only two cases where the same investigators used the same methods to estimate snow leopard population across multiple years (Jackson et al., 2006; Sharma et al., 2014). Also, Jackson et al. (2006) used different sized study areas across the 2 years.

Snow leopard densities were plotted against their effectively sampled areas. To assess the impact of the study area size on estimated snow leopard population density, we modelled snow leopard density using Equation (1).

$$Y = c + a \times \exp(-b \times X) \quad (1)$$

Here, c is the constant that indicates the value of snow leopard density when sampled area is very large and density has plateaued. The rate of decay is indicated by b and $a + c$ is the y-intercept. Estimated snow leopard density is indicated by Y and effectively samples area by X . We estimated the required study area size as a function of the SE of c using Equation (2) by re-arranging the terms in Equation (1). All the analysis was conducted in R (R Core Team, 2015).

$$\text{Study area size} = (1/b) \times \log(SE/a) \quad (2)$$

2.2 | Simulations

We used camera trap data from a study site of 1,684 km² in the Tost Nature Reserve in Mongolia to simulate the trends in density of snow leopards with increasing size of sampled area (see Sharma et al., 2014 for details of study site and fieldwork design). We estimated density using the maximum likelihood spatially explicit capture–recapture (ML SECR) method (Borchers & Efford, 2008) using the “secr” package in R (Efford, 2018; R Core Team, 2015). We conducted two types of simulations. In set A, we sub-sampled these data to derive estimates of snow leopard population density for a varying size of the sampled area, ranging from 81 to 1,684 km². We sub-sampled rectangular study areas progressively increasing from the center of the study site (Figure 2). The idea was to understand if there is a change in snow leopard density estimate with increase in the size of effectively sampled area. Also, in this set, we started from the center of the study area which was likely to represent better snow leopard habitat. We aimed to assess the impact of small study size together with that of sampling bias towards better quality habitats.

In set B, we again estimated snow leopard density along a range of study area size ranging from 81 to 1,684 km². However, in this set, each sub-sample was randomly located (Supporting Information Figure S1). Here, we wanted to assess the impact of the study area size without bias in study area site selection. We did 100 simulations with a random start location and randomly chosen area between 81 and 1,684 km². We tried a range of buffer sizes from 5 to 50 km at intervals of 5 km to each sub-sample in both sets. The buffer size where density estimates stabilized for each sub-sample was used for that sub-sample.

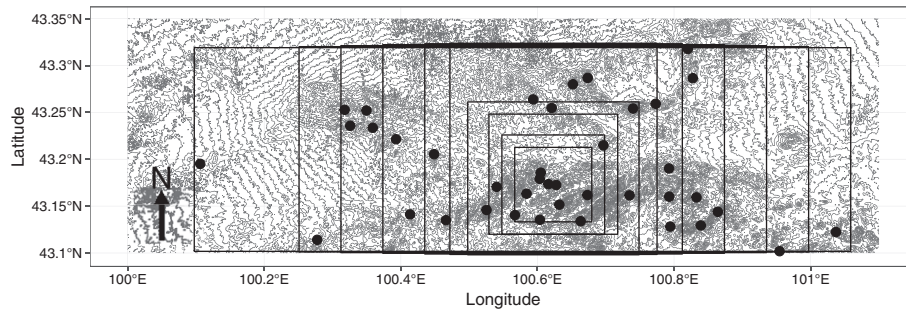


FIGURE 2 Analytical design used for examining the relationship between estimated snow leopard density and size of the sampled area in simulation set A. The dots indicate camera trap locations in Tost Nature Reserve, South Gobi, Mongolia. We estimated snow leopard density for varying size of sampled area, ranging from 81 to 1,684 km² by sub-sampling cameras in concentric rectangles as shown. The grey lines indicate 10 m contours. The sampled areas in published studies on snow leopard abundance range from 60 to 1,684 km², with a median of 375 km²

3 | RESULTS

3.1 | Literature review

A total of 17 studies of snow leopard population estimation using camera traps or faecal genetics have been published in peer reviewed literature (Table 1). These studies were conducted in 24 different sites in 6 of the 12 snow leopard range countries, and some of them were replicated over time (see Table 1 & Figure 1). The Tost Mountains of South Gobi, Mongolia, alone was sampled eight times. We found only one study where camera traps were placed in supposed snow leopard habitat for population estimation but there were no snow leopard captures (Buzzard, Li, & Bleisch, 2017). One study (Janečka et al., 2008) was aimed at optimizing molecular markers to identify snow leopard individuals from scat samples and did not report the size of the study area and another study estimated density using pug-marks and radio-telemetry (Oli, 1994). These three studies were excluded from further analysis.

Countries for which no peer reviewed estimates were available included Russia, Kazakhstan, Uzbekistan, Afghanistan, Pakistan and Bhutan. Estimates were largely missing from major mountain ranges such as Hindu Kush, Karakoram and Kunlun Shan. The remaining 14 studies, some replicated in time, yielded 32 different estimates of snow leopard population for a total area of 9,596 km² (0.3–0.9% of snow leopard distribution range). The study area sizes ranged from 60–1,684 km², with mean and median size being 607 and 393 km², respectively. Only seven studies reported density estimates (contributing 17 estimates covering 14 sites and 6,672 km² or 0.2–0.6% of snow leopard global distribution range). The remaining seven studies only reported estimated abundance. These seven studies contributed 15 estimates. A total of 18 estimates were from within PAs and the rest 14 from outside. Density estimates in relation to study area size are shown in Figure 3.

The model of snow leopard density expressed as a negative exponential function of the sampled study area size (Density $\sim 0.78 + 10.90 \times \exp(-0.01 \times \text{effectively sampled area})$) explained 79.2% of the variation in snow leopard

density (Figure 3). The negative exponential flattened out at snow leopard density of 0.79 ($SE = 0.28$) per 100 km² (the constant c), corresponding to a study area size of 481 km², for the predicted density value to be within one SE of c . Similarly, the model estimated that sampled areas should be at least 573 km² to be within half the SE on the higher side of the predicted density for very large study areas. We found that 55% (17) of the estimates had an effective study area of below 481 km².

We found no significant difference in estimated snow leopard density between protected ($n = 18$) and non-PAs ($n = 14$) (t -value = 0.21, $n = 32$; $p = 0.83$). The mean reported density of snow leopards from PAs and non-PAs was 2.13 and 2.30 per 100 km², respectively. Additionally, we found that although mean snow leopard density estimated by studies using spatially explicit capture-recapture

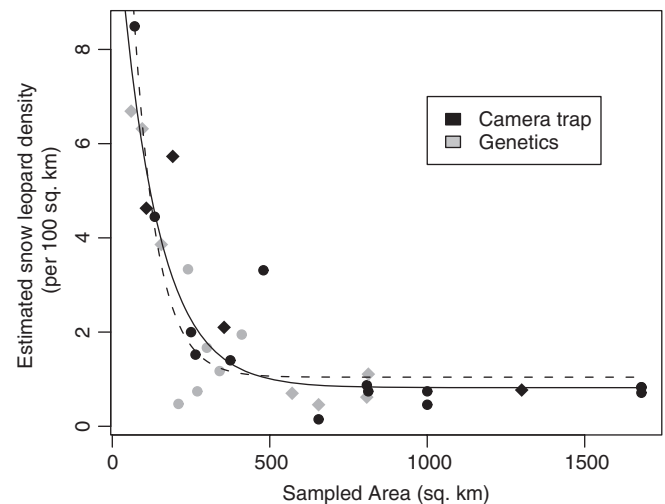


FIGURE 3 Snow leopard population density plotted against the size of sampled area. Black dots represent studies that used camera trapping ($n = 18$) while grey dots indicate molecular genetics ($n = 13$) sampling. The diamonds indicate studies which only estimated the abundance of snow leopards and had not attempted to estimate density ($n = 11$), while circles represent studies that estimated density of snow leopards ($n = 20$). The continuous line is the negative exponential model fitted to the entire dataset while the dotted line is the model fitted to only those studies that estimated density

methods (mean = 1.48, $SE = 0.64$) appeared lower, but the difference was not significant compared to estimates of snow leopard density in studies using half MMDM or full MMDM (mean = 2.53, $SE = 1.12$) or crude estimates (mean = 2.27; $SE = 0.47$). Only 4 out of the 32 snow leopard population estimates in literature were based on spatially explicit mark–recapture methods.

Our simulation exercise on the camera trap data from Tost Mountains showed that the estimated snow leopard density declined as the study area size increased in cases where the sub-sampled site included the center of the landscape, that is, where sampling was biased towards better quality habitat (set A). The density estimate (1.63/100 km²) for the smallest sub-sample (81 km²) was over five times higher (0.347/100 km²) than the estimate for the largest scale (1,684 km²) (Figure 4a). However, the declining trend did not show an exponential pattern as we found in the meta-data. The estimated abundance of snow leopards ranged from 8 to 18 individuals from the smallest to the largest sub-sample. We did not see such a decline in snow leopard density with increasing study area size in set B where the sub-sample was chosen at random and was not biased towards better quality habitat (Figure 4b). The mean estimated snow leopard density was 0.9/100 km².

4 | DISCUSSION

Our review shows that in the case of snow leopards, much uncertainty exists regarding the two most basic attributes that are critical for assessing the status of any threatened species: the size of the distributional range, and its population. One of our primary objectives was to assess the potential of data gathered from existing studies for estimating the global population of snow leopards. We found that these studies are inadequate for a variety of reasons: (a) geographical coverage of countries and mountain ranges in existing studies is highly skewed, (b) the real coverage of existing studies is minuscule (0.3–0.9%) compared to the presumed size of the global distributional range of snow leopards (1.23–3.02 million km²) and (c) the study area sizes in 55% cases are not large enough (481 km²) and likely overestimate snow leopard abundance considerably.

The small size of sampled areas together with a bias towards good quality habitats in many studies may overestimate density by up to five times. Our meta-analysis found that field studies with small study area size systematically lead to over estimation of snow leopard density. Together with our results from the simulation study, this suggests that field studies are biased towards good quality snow leopard habitat. The overestimation in small areas likely happens because studies lean towards sampling in sites with relatively high snow leopard density (or hotspots) within the larger landscape, as researchers tend to look for and sample in the best habitats to maximize captures. Hotspots are areas

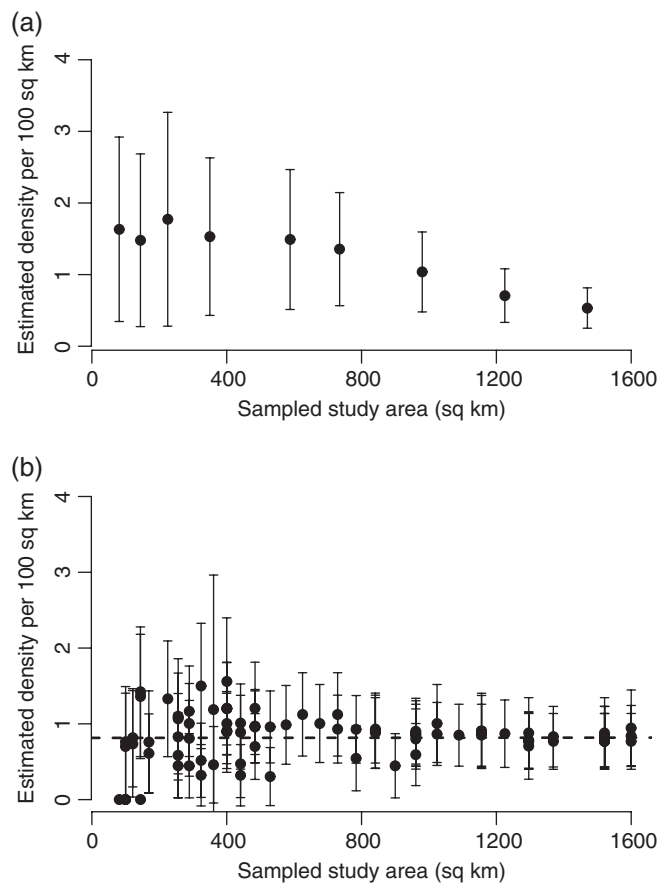


FIGURE 4 (a) The estimated snow leopard density using spatially explicit capture–recapture (SECR) in relation to increasing study area size when the center of the sub-sampled area was the same as the center of the larger study site (set A in methods). (b) The estimated snow leopard density in relation to increasing study area size when the center of the sub-sampled area was chosen at random (set B in methods). The estimates were obtained by sub-sampling actual camera trap data from Tost Nature Reserve, Mongolia. Error bars represent estimated 95% confidence interval in both panels

where home-ranges of multiple snow leopards show some overlap owing to high local prey densities or due to local geomorphology (Johansson et al., 2016). There may also be methodological issues when study areas are very small in relation to the home range size of the animal. Our results suggest that study areas be at least 481 km² in size for the density estimates to stay within 1 SE of the predicted density for very large areas. This may be particularly relevant in the case of the snow leopard, where 55% of the study sites were smaller than the home range of just two adult male snow leopards (Johansson et al., 2016).

While larger study area size is always desirable, many studies are limited by resources and logistics of covering large areas. Further, the SECR method requires sampling to be conducted more densely to obtain sufficient recaptures of individuals on multiple cameras, thus resulting in better estimates the ranging parameter sigma (Sollmann et al., 2013; Wilton et al., 2014). This can lead to further reduction in the area that field teams can cover. Our results from the simulations suggest that the small size of the study area is not as

much a problem for over-estimation if the bias in the choice of the study area can be addressed. Hence, field studies that are likely to sample smaller areas should be especially mindful to not bias their sampling to the best habitats, particularly if the population estimates are desired to be representative of larger landscapes and are meant to contribute to global population assessments. Conversely, global assessments of snow leopard population should not use the estimates from smaller areas where they are biased towards good quality habitats. To improve global estimates, we recommend coordinated surveys across large landscapes together with information on covariates to be analysed using spatially-explicit capture–recapture (Royle, Sutherland, Fuller, & Sun, 2015; Sutherland, Fuller, & Royle, 2015). Combining information on home range from telemetry studies and integrating data from camera trap and scat based genetics can further improve population estimates when analysed using SECR methods (Sollmann et al., 2011, 2013; Sollmann, Gardner, et al., 2013).

We did not find any difference in snow leopard population densities estimated inside and outside PAs. This finding supports the idea that snow leopard conservation needs a landscape-level, land-sharing approach that looks well beyond PA boundaries (Johansson et al., 2016; Mishra et al., 2018). A recent study on occupancy of snow leopards in India has similarly reported high probability of snow leopard occurrence outside PAs (Ghoshal et al., 2017). However, this and other studies have also shown that large parts of potential habitat are actually devoid of any snow leopards (Bai et al., 2018; Ghoshal et al., 2017; Taubmann, Sharma, Jumabai Uulu, Hines, & Mishra, 2016). This is reinforced by the wide range of figures we obtained in literature regarding the presumed size of the global distributional range of snow leopards. Thus, to foster a better understanding of global snow leopard population, it is essential that sampling be conducted in representative sites both inside and outside Protected Areas.

Mean snow leopard density estimated using spatially explicit capture–recapture methods was lower than estimates using other methods, however, this difference was not statistically significant. It has been shown that SECR based population estimation is more precise and robust and conceptually superior in comparison to other methods (Efford & Fewster, 2013). Studies have generally found that traditional non-spatially explicit methods tend to over-estimate animal densities (Ivan, White, & Shenk, 2013; Rich et al., 2014). In our case, the lack of statistical significance was probably due to the relatively small samples size, as few estimates are available for snow leopard density, and due to the large variation in density estimates.

We found that no peer-reviewed estimates of snow leopard abundance exist in half (six) of the snow leopard range countries. Efforts have largely concentrated in India (8 estimates), Mongolia (8), China (5) and Kyrgyzstan (4). Important mountain ranges such as Hindu Kush, Karakorum and Kunlun Shan do not have any published studies and large

part of the Tibetan plateau is under-represented (Figure 1). Additionally, we found that studies of snow leopard population estimation cover just 0.3–0.9% of the presumed global snow leopard distribution range. Therefore, we conclude that existing studies of snow leopard population densities are spatially inadequate and the existing estimates tend to be biased towards estimating higher snow leopard densities because of the tendency of sampling small areas and the use of non-SECR methods of analysis.

Widespread use of camera trapping in a photographic capture–recapture framework has yielded most comprehensive country-wide surveys estimating Tiger (*Panthera tigris*) abundance in Bhutan, India and Nepal between 2013 and 2015 (Dhakal et al., 2014; Jhala, Qureshi, & Gopal, 2015). The non-invasive, relatively cheap and easy to operate technology of camera trapping has allowed for coverage of more trap locations, longer durations, newer sites and larger areas. Despite such a huge effort, Harihar, Chanchani, Pariwakam, Noon, and Goodrich (2017) noted that the supposed 22% increase in global tiger population reported by these surveys was questionable due to unreported methods, lack of comparable baselines, failure to adjust population estimation to account for increased survey efforts, and inconsistent modelling processes. For instance, an increase in sampling effort between the 2010 and 2014 national tiger surveys in India actually resulted in a lower estimate of tigers in 15 of the 24 sites sampled in both the surveys. Generally, this happens when initial study areas are centred on regions of known species occurrence and then expanded to include low density areas. Thus, despite several methodological advances, estimates of large carnivore densities at meaningfully large spatial scales are rare and can face methodological inadequacies (e.g., Dey et al., 2017).

Our results suggest that arriving at an unbiased global estimate of the snow leopard population will require sampling larger and newer areas and a refinement of the global distribution range map. The current state of population studies also calls for an urgent need to refine sampling and analytical protocols for snow leopard population estimation at large spatial scales. The effort to estimate snow leopard distribution and population across its range will require agreement and cooperation amongst researchers, conservationists and governments. It will need to ensure consistent methodology, and strictly adhere to the basic principles of sampling theory. In this regard, we welcome and underpin the recent agreement of the 12 snow leopard range country governments to initiate and support a new collaborative exercise called PAWS, or Population Assessment of the World's Snow Leopards (The Bishkek Declaration, 2017).

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Author contributions

K.R.S. conceived the idea, conducted the literature review to put together the meta-data, analysed the data and contributed to the writing of the manuscript. C.M. helped develop the ideas, guided the analysis and contributed to the writing of the manuscript. M.K. helped with literature review for meta-data, analysis and contributed to the writing of the manuscript. K.S. contributed camera-trap data and commented on the manuscript. P.L. contributed to camera trap field work.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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