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Land sharing is essential for snow leopard conservation

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ABSTRACT

Conserving large carnivores in an increasingly crowded planet raises difficult challenges. A recurring debate is whether large carnivores can be conserved in human used landscapes (land sharing) or whether they require specially designated areas (land sparing). Here we show that 40% of the 170 protected areas in the global range of the snow leopard (*Panthera uncia*) are smaller than the home range of a single adult male and only 4–13% are large enough for a 90% probability of containing 15 or more adult females. We used data from 16 snow leopards equipped with GPS collars in the Tost Mountains of South Gobi, Mongolia, to calculate home range size and overlap using three different estimators: minimum convex polygons (MCP), kernel utility distributions (Kernel), and local convex hulls (LoCoH). Local convex hull home ranges were smaller and included lower proportions of unused habitats compared to home ranges based on minimum convex polygons and Kernels. Intra-sexual home range overlap was low, especially for adult males, suggesting that snow leopards are territorial. Mean home range size based on the LoCoH estimates was 207 km^2 ± 63 SD for adult males and 124 km^2 ± 41 SD for adult females. Our estimates were 6–44 times larger than earlier estimates based on VHF technology when comparing similar estimators, i.e. MCP. Our study illustrates that protected areas alone will not be able to conserve predators with large home ranges and conservationists and managers should not restrict their efforts to land sparing.

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1. Introduction

Maintaining viable populations of large carnivores is a major challenge for biodiversity conservation because carnivore food requirements and extensive spatial needs often conflict with human interests (e.g. Treves and Karanth, 2003). In contemporary conservation planning these challenges are manifested in two paradigms, the "coexistence" (land sharing) and the "separation" (land sparing) models (Fischer et al., 2014; Chapron et al., 2014). Both approaches face considerable challenges; land sharing requires human activities to be tolerant enough towards biodiversity, including species that pose a risk to life or property (e.g. livestock), whereas land sparing requires large enough areas to be set aside exclusively for conservation. Although large carnivores can persist in human-dominated landscapes when attitudes and policies are favorable (Linnell et al., 2001; Chapron et al., 2014), challenges posed by conflicts associated with livestock killing, competition for game animals and attacks on humans must be addressed to ensure long-term coexistence (Inskip et al., 2009; Johansson et al., 2015). For land sparing, the size of the protected areas is a key predictor of success in conserving large carnivore populations (Balme et al., 2010; Woodroffe and Ginsberg, 1998). However, land sparing may be inefficient (Liu et al., 2001; Rauset et al., 2016) or not possible when land is expensive or when human exclusion has substantial negative impacts on affected people (Schmidt Soltau, 2003; Bauer et al., 2015).

The relative emphasis needed on either approach for conserving a target species largely depends on the species' spatial requirements and social organization. This is because long-term population viability will be determined by: (1) the key drivers of population growth (survival and fecundity), which are a function of habitat quality, including human factors, and (2) stochastic population extinction risk, which will be a function of population size (Caswell, 2000). Thus, key parameters in predicting the size and location of adequate spared land for maintaining viable populations of a target species are its home range size,

territoriality, and habitat suitability. In most solitary carnivores, males have larger home ranges than females (Sandell, 1989), and it is therefore necessary to estimate sex-specific home range sizes. Similarly, home ranges can be overlapping or exclusive, which can strongly influence how many individuals occupy an area. Understanding home range size and social organization is critical for predicting the number of animals that can be sustained within conservation areas, and thus for predicting long-term population viability (Balme et al., 2010; Woodroffe and Ginsberg, 2000). Animals with small and overlapping home ranges will require less land than animals with large and/or non-overlapping home ranges. Home range use is also related to habitat quality which is an important determinant of survival and reproduction (Schwartz et al., 2006). With advances in animal tracking technology, it has now become possible to obtain relevant data to understand the spatial ecology of large carnivores and feed the information into conservation planning (Schwartz et al., 2006; Balme et al., 2010).

Snow leopard (*Panthera uncia*) distribution spans 1.2–1.6 million km^2 of high mountain habitat in 12 countries of central Asia (Jackson et al., 2010). Snow leopards primarily share the landscape with livestock herders and only a small proportion of the species' range (14–19%) is set aside in protected areas (Deguignet et al., 2014). The snow leopard is classified as endangered by IUCN, where the main threats to the species are retaliatory killing in response to livestock predation, poaching for trade in fur and bones, depletion of wild prey, and habitat degradation and fragmentation resulting from mining and development (Jackson et al., 2008, 2010). It is not clear how effective protected areas are for snow leopard conservation because published information on snow leopard spatial ecology is limited to three studies (Jackson, 1996; Oli, 1997; McCarthy et al., 2005) that were all based on few individuals (n = 3–5) equipped with VHF collars. The information obtained from VHF collars may not be adequate for snow leopards, as preliminary information from studies using Global Positioning System (GPS) technology in three different countries (Afghanistan, Pakistan and Mongolia) suggests that snow leopard home ranges may be substantially larger than earlier studies have reported (Johansson et al., 2016). To better assess the scale and land tenure (sharing vs. sparing) where conservation efforts need to be focused, it is critical to obtain accurate information on the spatial requirements and social organization of snow leopards.

To achieve this goal we fitted snow leopards of both sexes with GPS collars in Tost, a mountain range in southern Mongolia that was declared as State Reserve in 2016 but was a multiple use area during data collection for this manuscript. Our aims were to (1) generate robust and biologically relevant estimates of sex-specific home range size for snow leopards, (2) estimate the extent of home range overlap for neighbouring individuals to examine territoriality, and (3) compare the size of protected areas throughout the snow leopard range with the home range size of adult snow leopards to assess if snow leopard conservation can rely on current protected areas or if a land sharing approach is required to conserve the species.

2. Materials and methods

2.1. Study area

The study was conducted in the Tost Mountains in the Gobi Desert of southern Mongolia (43°N, 100°E, Fig. 1). The area consists of several mountain massifs, crisscrossed by canyons and steep ravines. The mountains gradually shift from steep cliffs in the centre to more gentle hills in the periphery followed by steppe, with an altitude range between 1600 m and 2500 m above mean sea level. Annual precipitation is <130 mm/year and expected min and max temperatures are −35 °C to 38 °C with strong winds year around. The snow leopard population in Tost has been estimated to be 10–14 adult individuals (Sharma et al., 2014). Approximately 90 semi-nomadic herder families live in the mountains and surrounding areas; their livestock comprise of goats (*Capra aegagrus hircus*), sheep (*Ovis aries*), camels (*Camelus bactrianus*) and horses (*Equus ferus caballus*). The snow leopards prey mainly on Siberian ibex (*Capra sibirica*), domestic goats and argali sheep (*Ovis ammon*) (Johansson et al., 2015).

2.2. Data collection and study animals

Snow leopards were captured in foot snares set at marking sites and immobilized with a combination of medetomidine and tiletamine-zolazepam (see Johansson et al., 2013 for details of capture procedures). They were equipped with GPS collars (North Star, King George, Virginia, USA, 2008–2009 or GPS-Plus, Vectronic Aerospace, Berlin, Germany, 2010–2014). The North Star and Vectronic collars were programmed to take a GPS fix every 7 and 5 h respectively. We include information from only those snow leopards that were followed for more than
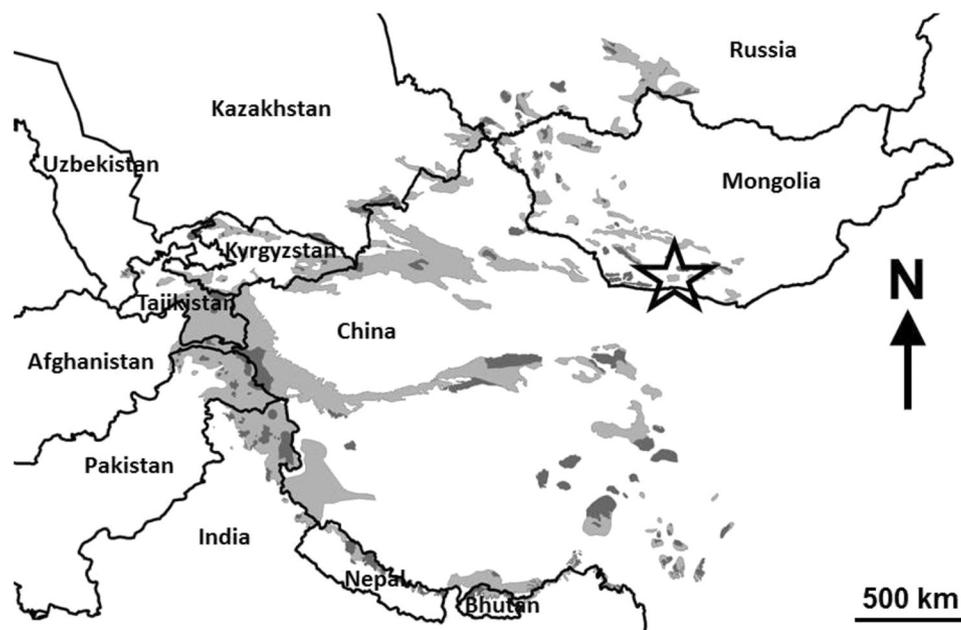

Fig. 1. The global snow leopard (*Panthera uncia*) distribution classified as definite or probable occurrence (light grey; McCarthy et al., 2016), protected areas in snow leopard habitat (dark grey; Deguignet et al., 2014) and the location of the study area (star) in Tost Mountains in the Gobi desert of southern Mongolia.

three months (n = 16). Data from relatively young individuals, collared when they were still associated with their mother, were truncated to include only the period after they separated and their movements became independent of their mother's.

Age of the captured snow leopards was estimated based on body mass, teeth coloration and wear. In addition, males were examined for facial scars and individuals that lacked scars were assumed to be young males (2–3 years old) whereas scarred males were considered >3 years. Similarly, females that did not show signs of previous reproduction in colouration and size of nipples were judged to be 3 years or younger and were classified as subadults. Females that had reproduced were assumed to have darker and larger nipples than females that had not reproduced (Brooks and McRoberts, 1997).

2.3. Estimating home range size and habitat within home ranges

The GPS location data for individual snow leopards varied in duration (number of days) and location frequency, which can influence home range estimates (Börger et al., 2006). We therefore standardized the data by removing missing locations (i.e. unsuccessful attempts on GPS fix) as well as erroneous locations and outliers using the sample script provided by Bjørneraas et al. (2010) with movement metrics adjusted for snow leopards (D = 100,000 m; m = 25,000 m; a = 5000 m/h; q = −0.97). We also randomly selected 3 positions per individual per day. Locations collected during dispersal (22 and 4 locations for two individuals) were removed as these represented cases of substantial extra-range movement. We used net squared displacement (Bunnefeld et al., 2010) in R package adehabitatLT (Calenge, 2011) to identify data driven temporal break points in space use behaviours and home range shifts instead of pre-defined break points such as annual home ranges. We observed behavioural shifts in the space use among individuals of both sexes around the age of 3 years when they tended to settle in home ranges that were more stable over time. At this point, i.e. when establishing permanent home ranges, individuals were classified as adults, thus some individuals were observed in two demographic groups (subadult and adult, Table S1).

We used three different home range estimators to analyse the snow leopard data; minimum convex polygon (MCP), fixed kernel (Kernel) and local convex hull (LoCoH). MCP and Kernel are the two most commonly used estimators (Fieberg and Börger, 2012). While Kernel is considered more accurate than MCP (Börger et al., 2006), both have been criticized for including areas that are not used by the animals (Getz and Wilmers, 2004; Getz et al., 2007). This may be especially true when the home ranges have sharp boundaries, i.e. the border is formed by non-habitat such as water bodies for a terrestrial species. In such situations the LoCoH has been shown to be more accurate than the other estimators (Getz et al., 2007). We included all three estimators to provide the most accurate estimates and to compare our results with earlier studies. We estimated 95% MCPs and 95% Kernels (bivariate normal smoothing curve and h_{REF}*0.6) in the R package adehabitatHR (Calenge, 2006). Adaptive local convex hulls (aLoCoH) were estimated using the R package TLoCoH (Lyons et al., 2013). As we analysed static aLoCoH ranges and not spatiotemporal dynamics, the temporal parameter s was set to 0. We applied a range of levels for the parameter a (based on the heuristic a_1), plotted individual home range sizes against a, and identified a = 25,000 as a suitable break point for aLoCoH ranges (Getz et al., 2007).

To evaluate potential spurious effects of number of radio days, number of locations, and fix rate (i.e. average number of locations per day) on home range size, we initially fitted linear models separately with each variable and compared AICc to the null model (Burnham and Anderson, 2002). None of these variables had support (tested on aLoCoH estimates) and were therefore not included in later calculations: number of radio days (ΔAIC_C = 2.26), number of locations (ΔAIC_C = 2.63), average number of successful GPS fixes per day (ΔAIC_C = 1.37). We tested for variation in home range size (aLoCoH)

in relation to demographic group (female adult, female subadult, male adult, male subadult) of snow leopards with linear mixed models in R package lme4 (Bates et al., 2015). Animal ID was included as random factor to control for repeated observations where the same individual shifted home range or age category.

To evaluate how well the different home range estimators reflected snow leopard space use, we compared the proportion of mountain and steppe habitats within the respective home range maps obtained from each estimator, with the proportion of GPS locations within the two habitat types for each individual. Elevation data were obtained from a Digital Elevation Model (ASTER DEM with 30 m resolution), and analysed in ArcGIS 10.1 (ESRI, Redlands, CA.) We calculated topographic ruggedness in a 3×3 neighbourhood using the Vector Ruggedness Measure (Sappington et al., 2007), and divided the resulting layer into mountains (high VRM) and steppe (low VRM) using Jenks natural breaks. We then calculated the proportion of mountain and steppe for (1) home ranges using the intersect function and (2) GPS positions using the spatial join function in ArcGIS.

2.4. Home range overlap

LoCoH estimates, considered more accurate to identify edges of home ranges than MCP and Kernel (Getz et al., 2007), were used to calculate overlap between home ranges. We calculated the proportion of overlap in aLoCoH between neighbouring snow leopards. Neighbours were defined as animals that overlapped in their locations for at least three months, and were separated by less than half the radius of average-sized home ranges for each sex and age category. For each neighbour pair, we calculated the proportion of home range overlap of individual X on Y and the proportion of home range overlap of individual Y on X, given that the size of home ranges (and thus proportion of overlap) differed among individuals. Similar to above, variation in home range overlap (aLoCoH) was tested in relation to demographic group with linear mixed models in R package lme4 (Bates et al., 2015), with Animal ID as random factor.

2.5. Home range size compared with the size of protected areas

A map of the global snow leopard range was derived in 2008 using a combination of published information, expert opinion, and an overlay of snow leopard observations with environmental layers (McCarthy et al., 2016). We combined this map, using the areas defined as definite and probable occurrence but excluding areas defined as possible occurrence, with a shape file derived from the most comprehensive global database of protected areas throughout the world compiled by UN and IUCN (Deguignet et al., 2014). This allowed us to calculate the proportion of each protected area that overlapped with snow leopard distribution using the intersect function in ArcGIS. We did not consider level of protection, as this information was not available for many areas.

We compared the size of protected areas in the snow leopard range with the average size of a male snow leopard home range (aLoCoH), and with 15 randomly drawn home range sizes of adult females (aLoCoH and MCP with no overlap and with overlap of two neighbours). To account for the possibility that home ranges may be smaller in parts of the distribution range, we repeated the comparison with a 50% reduction of home range size (aLoCoH). The female home ranges were drawn from a Gamma distribution with 1000 iterations. The shape parameters for the Gamma distribution (α and β) were calculated from mean home range size and standard deviation for adult females. These simulations yielded the number of protected areas that had ≥90% chance to contain at least 15 adult females. We recognize that 15 females do not constitute a long-term viable population considering stochastic events and potential inbreeding. However, we used it because it is estimated that a population must be of at least of this size to withstand human induced removal of one individual every second year (Chapron and Legendre, 2002).

3. Results

We obtained a total of 29,046 GPS locations from 16 snow leopards. After randomly selecting three locations per individual and day, 21,098 locations remained. The resampled dataset spanned a total of 8849 radio-days, representing an average of 2.4 locations/day, with snow leopards followed on average for 369 ± 213 (SD) days for each home range period (i.e. for one individual belonging to one demographic group and not shifting the location of its home range). Six of the 16 snow leopards were collared as both subadults and adults. One adult individual shifted home range (Table S1). The average fix rate was $66\% \pm 5$ SE. The outlier screening procedure removed 30 locations distributed among 10 individuals.

3.1. Home range size

The three home range estimators yielded diverging home range sizes, where the MCP and Kernel estimates were almost 3 times larger than the aLoCoH estimates (Table 1, Table S1). On average, the MCP and Kernel estimates were similar but for some individuals one or the other was substantially larger (Table 1, Table S1). The home range estimates using aLoCoH differed among demographic groups ($\Delta AIC_C = -25.4$). Irrespective of the estimator used, the pattern between demographic groups was similar, with adult males having the largest home ranges. Subadult females tended to have larger home ranges than adult females and adult females had similarly sized home ranges as subadult males (Table 1). The number of collared snow leopards that we monitored during the study ranged from 1 to 9 depending on trapping success and collar failures, see Table S1.

3.2. Habitat composition

Habitat composition, calculated as mean proportion of collar locations in each terrain type (75% mountains and 25% steppe), was more similar to the aLoCoH ranges (63% mountain and 37% steppe) than to the other home range estimators (MCP and Kernel; 50% mountains and 50% steppe for both). The habitat classified as steppe for the GPS locations and the aLoCoH ranges were generally small sections of steppe inside the mountain ranges, i.e. valleys, whereas the Kernel and MCP ranges included larger sections of steppe outside the mountains where no collar locations were obtained.

3.3. Home range overlap

Overlap in home ranges varied between demographic groups (ΔAIC_C 3.7). The lowest home range overlaps occurred between adults of the same sex. The overlap between adults of the opposite sex and between adults and subadults was larger (Table 2). Expectedly, the highest home range overlaps were between adult females and males. The home ranges of four female neighbour pairs (out of 24 pairs) and one male neighbour pair (out of 12 pairs) did not overlap and the mean distance between their borders was 1.0 km (± 1.1 SD, range

Table 1
Mean home range size (km$^2 \pm$ SD) for GPS-collared snow leopards (*Panthera uncia*) in Tost Mountains, Mongolia in 2008–2014.

Demographic group	MCP[a]	Kernel[b]	aLoCoH[c]	n
Female adult	327 ± 200	336 ± 136	129 ± 45	7
Female subadult	589 ± 83	554 ± 114	211 ± 87	4
Male adult	615 ± 319	617 ± 317	220 ± 84	9
Male subadult	474 ± 386	451 ± 265	141 ± 67	4
Average adult	489 ± 303	494 ± 286	181 ± 82	16
Average subadult	531 ± 266	503 ± 197	176 ± 81	8
Average snow leopard	503 ± 286	497 ± 255	179 ± 80	24

[a] MCP = 95% minimum convex polygon.
[b] Kernel = 95% fixed kernel utility distributions.
[c] aLoCoH = 95% adaptive local convex hull.

Table 2
Proportion of overlap between home ranges calculated with 95% adaptive local convex hulls (aLoCoH) of neighbouring pairs of GPS-collared snow leopards (*Panthera uncia*) in Tost Mountains, Mongolia in 2008–2014.

	Mean	SD	Min	Max	n
Female adult-female adult	0.17	0.19	0.00	0.55	24
Female adult-female subadult	0.36	0.18	0.15	0.58	6
Female adult-male adult[a]	0.50	0.30	0.00	0.96	17
Male adult-female adult	0.20	0.14	0.00	0.47	17
Male adult-male adult	0.17	0.14	0.00	0.51	12
Male adult-male subadult	0.33	0.24	0.02	0.68	8

[a] Home range size differs between the individuals which yields different overlap estimates, e.g. for adult male-adult female compared with adult female-adult male.

0.08–2.2 km). Despite the low overlap we identified two 'hotspots' in the central part of the study area that were used by five collared snow leopards simultaneously during two different time-periods (May 2011 to Feb. 2012 and Apr. to Aug. 2012) with a size of 8.4 km^2 and 19.7 km^2. These areas corresponded to 1% and 3% of the total area used by the five snow leopards.

3.4. Home range size in relation to size of protected areas

A total of 170 protected areas overlapped with the areas classified as definitely or probably inhabited by snow leopards. In these protected areas the amount of snow leopard habitat (definite and probable) ranged from 2 to 40,546 km^2 (mean = 1325 km^2, median 308 km^2). Among all these protected areas, 40% were smaller than the average home range (aLoCoH) of a single adult male snow leopard. The proportion of protected areas that were large enough to have a 90% probability of containing 15 or more adult females was 3% for MCP without overlap (shape parameters for the Gamma distribution; $\alpha = 2.7, \beta = 0.008$), 4% for MCP with overlap of two neighbours ($\alpha = 2.7, \beta = 0.01$), 12% for aLoCoH without overlap ($\alpha = 9.1, \beta = 0.07$), and 13% for aLoCoH with overlap of two neighbours ($\alpha = 6.3, \beta = 0.06$) (Table S2). When we reduced the home range size (aLoCoH) to 50%, the proportion of protected areas smaller than the home range of a male decreased to 24%. In addition the proportion of protected areas that had >90% chance to contain 15 or more adult females increased to 18% without overlap ($\alpha = 8.2, \beta = 0.13$) and 22% with overlap of two neighbours ($\alpha = 5.7, \beta = 0.11$).

4. Discussion

Understanding spatial ecology is fundamental for the development of conservation and management plans for wide-ranging animals such as large carnivores (Woodroffe and Ginsberg, 2000). Our study found: (1) substantially larger home ranges of snow leopards than previously published, estimates that are 6–44 times larger than VHF-based studies when comparing similar home range estimators (MCP Jackson, 1996; Oli, 1997; McCarthy et al., 2005), (2) evidence of territoriality with low overlap between adults of the same sex, and (3) that only a small proportion of the protected areas in the snow leopard range are large enough to support 15 or more adult females. In theory, a few very large protected areas could be enough to conserve the species, however even for the smallest home range estimate with overlap of two neighbours (i.e. the most generous estimate of how many snow leopards that can fit into a protected area) only eight of the existing protected areas were estimated to be capable of harbouring >50 adult females, all of which lie in the eastern end of the snow leopard distribution range (Table S2). These results highlight that snow leopards have a substantially larger spatial need than previously thought. The results also suggest that land sparing with protected areas forming the backbone of snow leopard conservation would not be sufficient to secure long-term and large-scale population viability. Even so, well-managed protected areas remain important as legally recognized protection

from damaging land uses such as mining or linear intrusions that can fragment populations or destroy habitats, as well as foundations from which larger protected areas can grow.

4.1. Home range size

Home ranges based on aLoCoH followed the mountain edges closely and were more similar in habitat composition to that of the GPS positions than the home ranges obtained from MCP and Kernel methods. We therefore conclude that aLoCoH yielded more biologically appropriate home range estimates for snow leopards. Even though snow leopards can traverse large areas of steppe when dispersing between mountain ranges (McCarthy et al., 2005), our radio-collared snow leopards rarely ventured out on the steppe, which reinforces that snow leopards are generally tied to mountains and that steppe is not considered prime habitat for the species (Jackson et al., 2010).

Previous studies of snow leopards have reported diverging patterns in sex-specific home ranges. Two studies reported female home ranges to be larger than those of males (Jackson, 1996; Oli, 1997), while McCarthy et al. (2005) reported the opposite pattern. In our substantially larger dataset, we found adult male home ranges to be about twice the size of the home ranges of adult females. This follows the general pattern observed across most solitary carnivores (Sandell, 1989; Duncan et al., 2015).

Large carnivore home range size is generally influenced by density, distribution, and predictability of resources, along with density of competing conspecifics (Nilsen et al., 2005; Duncan et al., 2015; Aronsson et al., 2016). Large felid species, such as tigers [(*Panthera tigris*) Goodrich et al., 2010] and leopards [(*Panthera pardus*) Stein and Hayssen, 2013], whose distribution range spans a large variation in these parameters, can exhibit vast divergences in home range size. Compared to tigers and leopards, in the case of snow leopards, we expect less variation in home range size between areas, given that they generally occur in low productivity habitats (Jackson et al., 2010). This is supported by preliminary findings from GPS-collared snow leopards in Afghanistan and Pakistan where reported home ranges were similar or slightly larger than in our study area (Johansson et al., 2016).

In addition to the ecological parameters that affect actual home range size, large variation between studies can also be explained by methodological differences. Substantial variation in home range size estimates can result from the estimators used, study duration, number of locations and sampling technique (VHF or GPS) (Girard et al., 2002; Fieberg and Börger, 2012). The use of VHF techniques for snow leopards requires considerably high effort in difficult precipitous terrain to relocate the animal with radio-signals that have a limited range. This can be difficult in mountains as obstacles such as hills easily block signals. All previous snow leopard studies reported significant periods of time when the collared animals could not be located, which suggests that the animals utilized a larger area than the tracking team could cover on foot in the inaccessible terrain. We hypothesise that differences in the ability to relocate snow leopards between VHF and GPS collars are the primary explanation for the large disparity in home range size estimates between studies.

4.2. Home range overlap and territoriality

Large carnivores are predicted to be territorial when food resources are stable and evenly distributed (Sandell, 1989) which coincides with the wild prey in our study area. It is difficult to document territory defence for large carnivores, therefore degree of home range overlap between neighbours is a proxy for territoriality (Powell, 2012). The intra-sexual home range overlap between adult snow leopards was low and suggests territoriality. This is exemplified by the home ranges of three adult neighbouring pairs, one male-male and two female-female, which were separated by 450, 200 and 80 m respectively without any apparent geographical barriers prohibiting overlap.

The home range overlap in our study differed markedly from that of previous studies on snow leopards where home ranges overlapped almost entirely (Jackson, 1996; Oli, 1997; McCarthy et al., 2005). Similar to above, we suggest that these differences are largely related to the difficulties in locating wide-ranging animals with VHF-collars in mountainous terrain although the social system may differ. It is also possible that individuals followed in those studies were repeatedly located in hotspots, creating a perception of high home range overlap. Both the hotspots we found in our study (where at least 5 adult snow leopards overlapped) were relatively small (4–15% of the average aLoCoH home range size). Whether high prey density or geospatial features lead to such hotspots is unclear and should be explored in future work. Differences in home range estimators may also have influenced the estimates of overlap in earlier studies. The LoCoH estimators have been developed more recently, and earlier estimates were based on MCP that tends to include areas not used by the animals (Getz et al., 2007).

We found high variation in intrasexual overlap. Among adult females, we recorded high overlap between a mother and her daughter (41% and 47%; illustrated in Fig. 2). High overlap of home ranges between related animals has been reported in other carnivores and may facilitate inheritance of home ranges (e.g. Goodrich et al., 2010). We do not have information on the relatedness among most of the individuals we studied. The highest overlap between adult males (31% and 51%) occurred in a situation when one male, M1, made an excursion into the home range of the other male, M3 (illustrated in Fig. 2). Shortly thereafter M3 died, and M1 abandoned his old home range and took over M3's range.

4.3. Conservation implications

Almost half of the protected areas in the global distributional range of the snow leopard are smaller than our estimate of the average home range of a single adult male and hence too small to hold a reproducing pair. This spatial mismatch probably occurs because few, if any, of these protected areas were created with the main purpose to save snow leopards. The database on protected areas that we used is the most comprehensive source of information on global scale compiled by IUCN and UN, even so we found some discrepancies between official size of protected areas and the size reported in the database collection. However, compared to the size of snow leopard home ranges these discrepancies were small and should not affect our conclusions. Irrespective of the home range estimator used (aLoCoH or MCP) or the number of overlaps (0 or 2), only a few (3–13%) protected areas were large enough to potentially harbour 15 females. Even in our sensitivity analysis where we simulated for home ranges that were half of the home range size of our estimates, there are only 22% of the protected areas that could harbour 15 females. Since we considered protected area size as a whole and did not separate their habitats into mountains and steppe, for this assessment, we believe that the MCP estimates are more appropriate because these home ranges incorporates an even mix of the two habitat types. Further, our simulations assumed that the protected areas were saturated by snow leopards, all individuals remained strictly within the borders, and that surrounding areas exerted no edge effects into the protected areas. Balme et al. (2010) showed that the density of common leopards declined from the core of a protected area towards the edges; that individuals closer to the border ventured outside protected area and had a higher risk of mortality compared to those close to the core. The fact that we constantly used the least rigorous assumptions in our choice set (i.e. the home range estimator that produced the smallest home ranges, no habitat classification of protected areas, the use of all parts of protected areas by snow leopards, all individuals remaining within protected area borders, and analysis with home range sizes assumed to be 50% smaller than our actual estimates) lead us to conclude that the lower range of our estimated
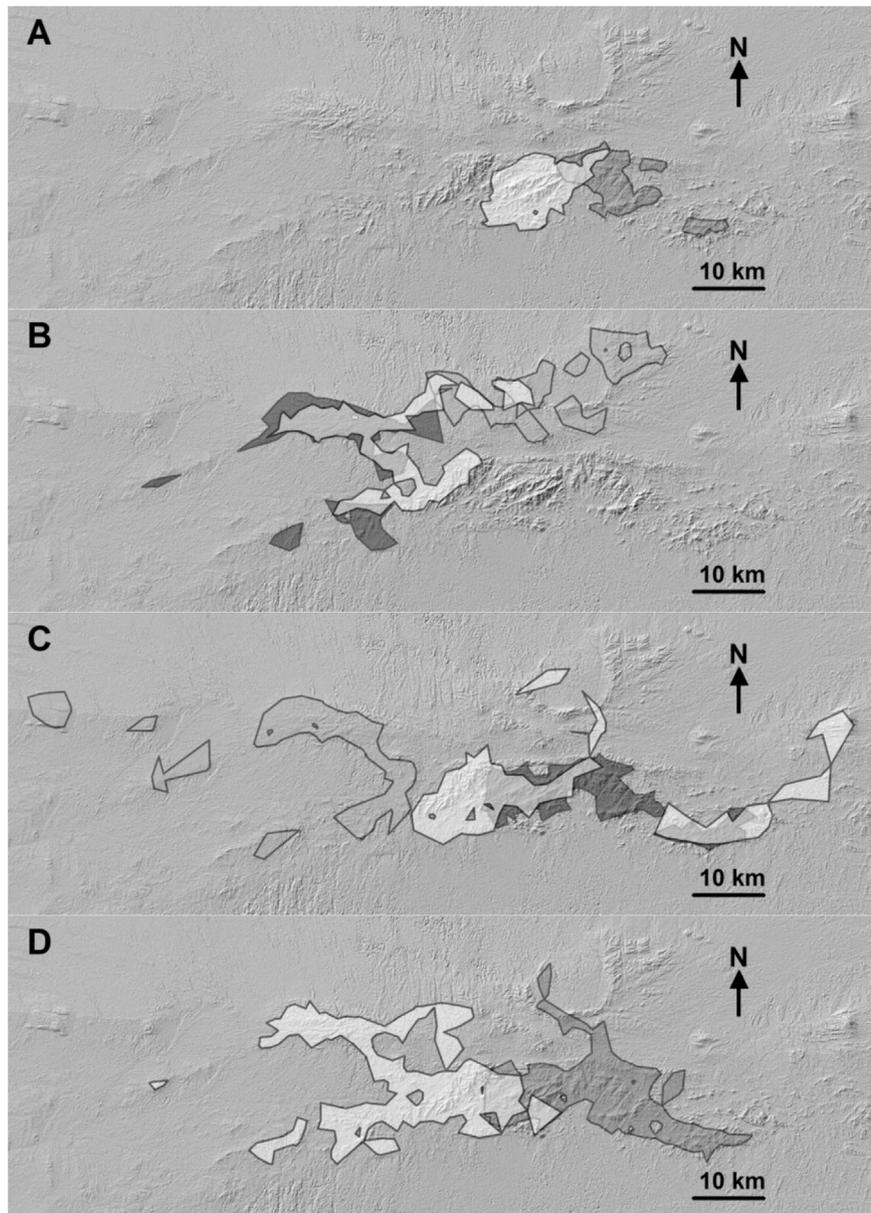
Fig. 2. Distribution and overlap of neighbouring snow leopards (*Panthera uncia*) in Tost Mountains, Mongolia, based on adaptive local convex hulls (aLoCoH). Data for individual snow leopards are presented in Table S1. A) Home ranges of two adult females (F3 in white and F4 in grey) in fall 2010 to spring 2011. B) The home ranges of three adult females from spring 2012 to spring 2013. The female illustrated in white (F8) was the daughter of the female illustrated in dark grey (F7). The distance between the home ranges of the females illustrated in dark and light grey (F9) was 80 m (i.e. zero overlap but bordering home ranges). C) Home ranges of three adult male snow leopards from July 2010 to March 2011. The male illustrated in white (M1) made an excursion east into the home range of the male illustrated by dark grey (M3) in late winter 2011 which resulted in 31 and 51% overlap between these two males (the highest in this study). The male M3 was found dead the month after the excursion and M1 subsequently took over his home range. The distance between the home ranges of the males illustrated in light grey (M4) and white was 450 m (i.e. zero overlap but bordering home ranges). D) Home ranges of two adult males from April 2012 to December 2012 (M1 illustrated in dark grey and M10 illustrated in white).

number of protected areas that can host 15 or more females is more realistic.

Our results show that conservation efforts for snow leopards cannot rely on protected areas (land sparing) alone. The large, exclusive home ranges we report suggest that for successful long-term conservation, managers must rely on a combination of land sharing and sparing, implemented at the scale of large landscapes. In this regard, the recent multi-governmental initiative called the Global Snow Leopard and Ecosystem Protection Program, that strives to secure snow leopard populations in large landscapes covering 25% of the global range of snow leopards through community-based conservation and green development is an important step towards long-term conservation of the species (Snow Leopard Working Secretariat, 2013).

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