Title: Landscape connectivity and population density of snow leopard across a multi-use landscape in Western Himalaya

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Short title: Spatial ecology of snow leopard

Abstract (300 words)

Human modification and habitat fragmentation significantly impact large carnivores requiring large, connected habitats to persist in a landscape. Understanding species responses to such change and the protection of critical areas and connectivity they provide is essential when planning effective conservation strategies. Our study examines the spatial distribution of snow leopard (*Panthera uncia*) across a gradient of protection status, anthropogenic pressures, and habitat types in the Gangotri landscape (~4600 km^2), Western Himalaya. Using spatial capture-recapture modeling, we analyzed a four-year camera trapping dataset (2015-2019) to assess the relationship between snow leopard movement and topography and identified the conducible areas for facilitating movement across the landscape. Snow leopard density was positively associated with elevation and slope and was higher in protected areas (summer: 1.42 SE 0.02/100km^2; winter 2.15 SE 0.03 vs. summer: 0.4 SE 0.01; winter: 0.6 SE 0.01 for unprotected areas). Precipitous terrain and several prominent mountain peaks were found to be resistant to snow leopard movement. Even with a range of human activities inside protected area, the higher density suggests a positive impact of protection. Density weighted connectivity showed that conducible areas are available between the Gangotri landscape and adjacent protected areas. However, compared to protected area, these areas are relatively less used and require attention for management. We recommend regulating human activities and co-managing pastures with local communities to revive prey base outside protected area, especially in corridors, to ensure such areas are functionally conducive. Our study provides a framework to collectively quantify the spatial pattern of abundance, distribution, and connectivity. Our approach has broad applicability for policymakers to develop strategic plans for balancing the conservation of species, and other land uses in a multi-use landscape.

Keywords

camera trapping, corridors, ecological distance model, Gangotri National Park, *Panthera uncia,* spatial capture-recapture

Introduction

Human modification has become the most dominant factor in range reduction and extinction of species worldwide (Ripple *et al.* 2014). Landscape modifications are particularly challenging for large carnivores because of their requirement for large areas (Crooks, 2002). Fragmentation-induced patch isolation negatively impacts gene flow, and demographic exchange, often leading to local extinction (Fahrig, 2003). Protected areas (PAs) may provide protection to carnivore populations by buffering them from anthropogenic impacts (Woodroffe, 2001), but due to their requirement for extensive areas, PAs alone are inefficient for the long-term conservation of large ranging carnivores (Hansen & De Fries, 2007). Landscapes outside of protected areas are therefore vital for facilitating dispersal and acting as a refuge for range-shifts resulting from changing climatic conditions (Forrest *et al.* 2012; Li *et al.* 2016). However, use and movement of species in human modified landscape depends on various factors for e.g. prey availability and human induced factors such as conflict, poaching and attitude of the locals (Ghoddousi *et al.* 2021). Consequently, conservation efforts for the recovery of threatened large carnivores require understanding and promoting co-existence with humans (Rio-Maior *et al.* 2019; Naha *et al.* 2020). Despite this, much of the current knowledge about large carnivore ecology derived from protected habitats, and an understanding of their ecology in multi-use landscapes is often lacking (Ripple *et al.* 2014).

Understanding the relationship between habitat use and spatial distribution of carnivores across human-modified landscapes is essential for planning effective conservation strategies (Zemanova *et al*., 2017). Investigating spatial patterns of abundance, distribution, and behavior of large carnivores in modified human landscapes is expected to reveal trade-offs resulting from the habitat requirements of species and their response to threats (Loveridge *et al.* 2017). Furthermore, effective conservation planning and management require additional information on corridors that facilitate dispersal across human-modified areas, prey species, and factors that can constrain access to such resources (Rio-Maior *et al.* 2019).

The snow leopard **(***Panthera uncia*), like many other large carnivores, is sensitive to anthropogenic pressures (Mishra, 2001; Namgail, Fox & Bhatnagar, 2007) and requires large tracts of habitat (Johansson *et al.* 2016). Despite its importance as a flagship species and indicator of ecosystem health (Snow Leopard Working Secretariat. 2013; Murali *et al.* 2017), the status of snow leopard is believed to be deteriorating across its range due to numerous anthropogenic pressures such as conflict (Suryawanshi *et al.* 2013, Maheshwari & Sathyakumar, 2020) poaching (Nowell *et al.* 2016) and decline in prey availability (Mishra *et al.* 2004). Published studies on snow leopard abundance are restricted only to 0.3–0.9% of the snow leopards' presumed global range (Suryawanshi *et al.* 2019, Sharma *et al.* 2021), and current information on snow leopard spatial ecology is inadequate for effective conservation planning and monitoring (Robinson & Weckworth, 2016; Suryawanshi *et al.* 2019).

Forty percent of the PAs within the snow leopards range are smaller than a single male's home range size; therefore, PAs networks alone are insufficient as an effective conservation strategy (McCarthy & Chapron, 2003; Johansson *et al*. 2016). Further, most PAs have a major portion of their area under permanent ice or glaciers and contribute little to the wildlife values directly (Bhatnagar, Mathur & McCarthy, 2001, Mishra *et al.* 2010). As a result, a large amount of wildlife may occur outside existing PAs (Bhatnagar, Mathur & McCarthy, 2001; Mishra *et al.* 2010). Moreover, very few PAs are free of human influence (Jackson *et al.* 2010). Grazing is practiced pervasively across its range, including PAs (Mishra *et al.* 2010). The high livestock density and associated declines in wild herbivore density can intensify the conflict between humans and snow leopard (Mishra *et al*. 2010). Persecution of snow leopard by pastoralists over livestock depredation is one of the major causes of species endangerment and a livelihood challenge for local communities (Mishra, Redpath & Suryawanshi, 2016). Given the large home range of snow leopard and people's high dependence on range lands, promoting coexistent is the only viable option for the continued survival of snow leopard in the region (Bhatnagar, Mathur & McCarthy 2001; Mishra et al. 2010). Hence, a widely recommended approach is to look beyond PAs and adapt a more extensive landscape-level approach (Bhatnagar, Mathur & McCarthy 2001).

The Project Snow Leopard (PSL) of India and Global Snow Leopard and Ecosystem Protection Program (GSLEP) aim to secure snow leopard population in large landscapes (PSL 2008, Snow Leopard Working Secretariat, 2013). GSLEP has identified 20 priority zones designed to conserve viable breeding populations and serve as a steppingstone for maintaining the snow leopard population (Snow Leopard Working Secretariat, 2013). However, these zones have been identified primarily based on expert opinion, and there have been few attempts to investigate fine-scale spatial densities of snow leopards and connectivity in these zones (Chetri *et al.* 2019; Li *et al.* 2020). We examined snow leopard density, distribution, and connectivity in one of the priority landscapes, Gangotri-Nandadevi landscape (Snow Leopard Working Secretariat, 2013). The study area represents a typical multi-use landscape with a gradient of habitat types, and human use. The landscape has one protected area (PA), Gangotri National Park, and previous studies suggest snow leopards are present in the area (Chandola, 2008; Bhardwaj, Uniyal & Sanyal, 2010; Rajvanshi *et al*. 2012; Pal *et al.* 2020), although baseline information about the population is deficient. Livestock rearing, agriculture, and tourism are the primary land-use types in the landscape. The present study was motivated by a lack of quantitative data on snow leopards in the region and limited knowledge of their distribution across various human land-use practices. Additionally, continuity between Gangotri and the other snow leopard habitats in the landscape is yet to be investigated, despite being central to its definition as a GSLEP core population.

Based on camera trap data on snow leopards over four years, our study assessed the density and connectivity responses to gradients of topographical and anthropogenic factors using a recent extension of spatial capture-recapture (SCR) models that allow for joint estimation of landscape connectivity and density. Our specific objectives were: (i) to identify seasonal, environmental, and anthropogenic drivers of variation in snow leopard density, (ii) to generate spatially explicit estimates of snow leopard densities across the landscape, and (iii) to identify potential areas important for connectivity in the landscape. We hypothesized that snow leopard densities would respond positively to the protection status and negatively to the presence of human settlements in the landscape. Human presence increases in summers in snow leopard habitats; therefore, we expected snow leopard density to differ spatially in summer and winter seasons. We also expected that snow leopard density would be higher in rugged and steep habitats as they are essential for hunting, resting, and escape cover (Chundawat, 1990; Fox & Chundawat, 2016; Johansson et al. 2016). Based on earlier studies on snow leopard movement (Chundawat, 1990; Fox & Chundawat, 2016), we expected snow leopard space use to be influenced by steep and rugged habitats. Derived from our results on fine-scale densities of snow leopard and dispersal opportunities, we discuss potential ways to design conservation landscapes. Our approach not only informs the conservation of snow leopard regionally but is also broadly applicable to other species requiring extensive areas often intermixed with humans use.

Methods

Study area

The upper catchment of Bhagirathi River, also known as Gangotri Landscape (~ 4600 km^2), is situated in the northeastern part of Uttarakhand state, Western Himalayan region of India (Fig. 1). The study area includes the Trans-Himalayan (Nelang valley) and the greater Himalayan region (Gangotri valley) of Gangotri National Park, and the greater Himalayan region of Uttarkashi Forest Division. Glaciers cover a large part (~755 km^2; Raina & Srivastava, 2008) of the study area (>5000m). The major vegetation types are alpine and subalpine vegetation (3,500–5,000 m) with Rhododendron spp., *Betula utilis* and alpine herbs, forb species, and temperate forest (2,500–3,500

m) with conifer species such as *Cedrus deodara*, *Pinus wallichiana*. The trans-Himalayan landscape consists of cold steppe vegetation such as *Caragana* sp., and *Lonicera* sp.. A weather station located inside the National Park (~3780 m.a.s.l) measured the mean annual maximum and minimum temperature (2000-2008) to 11.0°C and -2.3°C , respectively, and average winter snowfall of ~546mm (Bhambri *et al.* 2011). Snow leopards co-occur with other large carnivores: woolly wolf (*Canis lupus chanco*), Himalayan brown bear (*Ursus arctos isabellinus*) and common leopard (*Panthera pardus*). Potential prey species include Himalayan blue sheep or bharal (*Pseudois nayaur*), musk deer (*Moschus* sp.), Himalayan tahr (*Hemitragus jemlahicus*), goral (*Naemorhedus goral*).

In recent years, improvement of infrastructure and road connectivity for border security personnel has modified the area considerably. Gangotri valley inside the PA is an important pilgrimage site that has led to the establishment of a township near the source of Bhagirathi River. High altitude areas both inside and outside PA are tourist hotspots and grazing grounds for livestock (in summers). In 2019, ~ 18,800 tourists visited the PA (Forest department record). Around 30,000 livestock graze inside PA (except Kedar Tal and Gangotri) between May and September (Chandola, 2008). Compared to outside PA, human activities inside the park are well regulated and monitored by the forest department and paramilitary forces (RP pers. obs., 2015-2019). In winters (November to April), grazing is not practiced, and the PA remains closed for tourism, but paramilitary, few pilgrimages, and forest department are present. A previous analysis of seasonal anthropogenic pressure in the study showed a low presence of humans and associated activities in winters compared to summer, irrespective of protected status Pal et al. (2020).

Camera trapping

Camera trapping was conducted from 2015 to 2019, broadly covering two seasons: summer (May to September) and winter (November to March) (Table 1). Major valleys of the Upper Bhagirathi basin were accessed through trekking trails, herder's routes, or walking along rivers towards the origin (glacier). Each field expedition was usually conducted for 7-8 days, and each camera site could be visited only once per season due to logistic constraints. Cuddeback C1 camera traps were deployed along the elevation gradient of potential snow leopard habitat (3000-5000 m). Camera traps were deployed at a mean spacing of 1.72 km (SE 53.6 m) to simultaneously attain the twin objective of maximizing the chances of capturing different individuals and adequately recapturing individuals at different camera traps, as required in Spatial capture-recapture (SCR) design (Borchers & Efford, 2008). At each site, camera traps were deployed in locations likely to be used by snow leopard or prey species, affixed to trees or to a pile of stones, at a height of c.30–45 cm above the ground. We used a combination of both side and single side camera trap placement to maximize area coverage and identification of individuals. Outside PA, camera trap intensity was comparatively low than inside PAs due to the issue of camera trap theft.

Analysis

Identification of snow leopard individuals

Individual snow leopards were identified from camera trap pictures using their unique coat patterns. Individuals which could not be identified because of poor picture quality (e.g., blurry, overexposed) were excluded from the analyses. Sex was determined using cues such as the presence of visible genitals or presence of accompanying cubs. Cubs were excluded from the analysis. For the analysis, we used individuals for whom we captured on both sides, i.e., right and left flank (65%), and individuals with one side flank for whom we got maximum captures (right flank) (Augustine *et al*. 2018). Two-stage processing was done to identify individual snow leopards in each session: (i) for individuals with both flanks captured, each flank was separately analyzed and later cross-checked to confirm that the right and left flanks matched across sessions. This process could not be done for individuals with only right flanks, which contributed only 5% to the total captures (ii) the final identification of snow leopard individuals was cross-checked by two experienced researchers. Observer one and two were found to be 98% and 97% in agreement with the identifications of individuals. We addressed the doubts of both the observers to confirm the identity of the snow leopards. Photos without a final consensus were not included in the analysis. A total of 102 captures were discarded from the analysis. The first author's capability to distinguish between snow leopard individuals was tested using Snow Leopard Identification: Training and Evaluation Toolkit (https://camtraining.globalsnowleopard.org/leppe/login/). Observer accuracy (90.48%) using 30 trials was found sufficient for successfully identifying snow leopard individuals.

Spatial capture recapture model

We analyzed the resulting spatial encounter history data using SCR methods (Royle & Young, 2008) implemented in R using the package oSCR (Sutherland, Royle & Linden, 2019). To account for the fact that snow leopards are unlikely to have circular space-use patterns, we use the ecological distance SCR model that allows for non-Euclidean distance estimation (Royle *et al.* 2013; Sutherland, Fuller & Royle, 2015). Using this least cost path approach enables estimation of one or more resistance parameters (α_2) that quantify how movement is influenced by local landscape structure (Sutherland *et al.* 2019). Because sex is a partially observed individual attribute, we analyzed the data using the class-structured likelihood that allows for missing sex information (Royle *et al.* 2015).

SCR estimates density and space use from encounter history data y_{ijk}, a record of where individuals i were encountered in traps (having locations x_j) on one or more sample occasions k= 1,2,. . . K. The Euclidean distance SCR approach identifies a model for the observed encounters of individuals y_{ijk} as a latent process conditional on the activity centers s_i, represented by coordinates spread within the region of interest (state space, S). Binary encounter rate "detection/non-detection" at each trap are assumed to be Bernoulli trials: y_{ijk} ~Bernoulli(p_{ij}). Using the half-normal encounter function, the Euclidean distance model assumes that detection, p_{ij}, is a decreasing function of the Euclidean distance between trap locations x_j and the individual activity centers s_i, and hence, higher likelihood of detecting individuals at traps that are closer to an individual's activity center. The parameter σ is a spatial scale parameter that relates detection probability at a location x to distance from home range center s. The half-normal encounter model is:

$$p_{ij} = p_0 \times \exp\left(-\frac{d_{euc}(x_j, s_i)}{2\sigma^{\,2}}\right)^2$$

To estimate the density, the estimated number of individuals is divided by the state space (S) area (Royle *et al.* 2013). This model is based on Euclidean distance assumption i.e., space use is symmetric, circular and centered on the activity center (s) and is stationary without considering the location or surrounding landscape structure. An alternative to the euclidean distance model is the ecological distance model (Royle *et al.* 2013) that uses a least-cost path distance (d_{lcp}) based on a landscape covariate-specific resistance parameter (α_2). Based on resistance parameter, it is evaluated how a particular landscape covariate incorporated as discretized surface of pixel-specific covariate values influence space use by individuals which decided on the basis of by how much the observed spatial pattern deviates from the symmetric expectation (Royle *et al.* 2013, Sutherland *et al.* 2015). For all possible paths (w= 1, …, W paths) between υ and υ', $\mathcal{L}_w^{\upsilon,\upsilon'}$ consist of m_w path segments connecting $m_w + 1$ pixels. The cost-weighted distance between pixels is the product of the number of segments (length of path) and the associated cost of the landscape surface:

$$d_{\mathrm{lcp}}(\upsilon, \upsilon') = min_{\mathcal{L}_1, \ldots\ldots, \mathcal{L}_w} \sum_{\mathrm{p}=1}^{m+1} \mathrm{cost}(\upsilon_{\mathrm{g}}, \upsilon_{\mathrm{g}+1}) \times d_{euc}\,(\upsilon_g, \upsilon_{g+1}),$$

Where,

$$\mathrm{cost}(\upsilon_{\mathrm{g}}, \upsilon_{\mathrm{g+1}}) = \frac{\exp\left(\alpha_2 z(\upsilon_g)\right) + \exp(\alpha_2\, z(\upsilon_{\mathrm{g+1}}))}{2}$$

(Royle *et al.* 2013; Sutherland *et al.* 2015). Hence, by allowing for home range asymmetry that is explicitly linked to the surrounding landscape structure estimating α_2 represents a model-based characterization of the degree to which one or more covariate surfaces affects space usage within individual home ranges, that is, local connectivity at the individual scale (Sutherland *et al.* 2015).

Estimating density and movement of snow leopard

We defined the state-space (the area within which detectable snow leopard activity centers are expected to occur) as a regular grid of points using a 40 km buffer around the camera trap locations (large enough to include activity centers of all individuals exposed to detection on the cameras, Royle *et al.* 2013) and a resolution of 2 km (fine enough to approximate continuous space but coarse enough for computational tractability). Points that were deemed unsuitable (glaciers, >5300 m). i.e., that have a negligible probability of containing snow leopard activity centers, were excluded from the state-space). Snow leopard density was estimated for summer (May to September) and winter (November to March), henceforth referred to as 'session' (Table 1). For each session, duration for analyzing the density estimates was selected such that the conditions in terms of anthropogenic disturbance and season remained the same. Additionally, recent studies have shown that lengthening the data collection period in SCR studies is an effective way to increase the number of detections and improve the precision of estimates as long as it is timed to avoid peak recruitment periods (Dupont *et al*. 2019; Harmsen, Foster & Quigley, 2020). Hence, we used 5 months (152 -153 days) sampling for each session to optimize captures of snow leopard and minimize the risk of violating population closure. For understanding influence of terrain on snow leopard movement, we generated layers (1 km^2 resolution) of mean slope and ruggedness. We tested the effect of both Euclidean and ecological distance models on snow leopard movement and used the best model to fit rest of the parameters: density (D), detection (p) and space use (σ). We assumed negligible temporal variation in detectability within each session and collapsed all encounters into a single count. We modeled and tested density as a function of two temporal (session and season), three topographical (elevation, ruggedness, slope), one vegetation (Normalized Difference Vegetation Index) and two anthropogenic activity related (distance to human settlements and protections status) variables (Table 2). Detection probability was also examined for effect of sex, and camera trapping effort. Space use was modeled for sex and session. We selected models based on Akaike Information Criterion (AIC) (Burnham & Anderson, 2002). Pearson correlation tests were performed to examine any multicollinearity between covariates. The best model was used to predict realized density (number of individual activity centers per state-space pixel, Morin *et al.* 2017). Potential connectivity of a focal pixel was calculated as the expected frequency that the pixel is used by individuals located at every location in the landscape (source pixels) weighted by the distance between the focal and source pixel (via the estimated distance-dependent encounter function) and the expected density of the source pixel (via the expected density surface, Sutherland et al 2015, Morin et al. 2017). Finally, realized density and potential connectivity were combined to produce density-weighted connectivity (DWC)

(Sutherland *et al.* 2015; Morin *et al*. 2017). DWC represents the expected use of a pixel based on the known cost of movement and the estimated distribution of individuals in each landscape pixel (Sutherland *et al.* 2015; Morin *et al.* 2017) thus highlighting areas that are highly accessible from sites with high local abundance (Gupta *et al.* 2019).

Results

Camera trapping effort yielded 49,186 trap nights (PA: 44011; outside PA: 5175) and resulted in 713 identifiable snow leopard photographs out of 32,539 photos. Over the course of the sampling period, a total of 46 individuals were identified (6 males, 8 females, 32 unknown). Of these, 16 individuals were captured in more than four sessions and 18 were captured only in one session. Details on capture of snow leopard individuals for each session are provided in Supplementary information. Most of the captures of snow leopards were from inside the PA (98.6%). Outside the PA, snow leopards were captured from Srikant (5), Siyanghad (3), Kiyarkoti (1) and Gidara valley (1). For modeling the snow leopard density, we first tested models for movement parameter. The best-supported model for movement parameter was the model with slope as ecological distance. The conductance coefficient was estimated to be -0.52 (S.E = 0.043). Ecological distance model with slope was then used to fit density, detection, and spatial use of snow leopard. Correlation was (r>=0.7) between ruggedness and slope, elevation and distance from village, NDVI with elevation and NDVI with distance from village, and hence these predictor variables were not used together in models.

We tested 22 biologically meaningful models of which the top five models are shown in Table 3. Two models with Δ AICc < 2 were found. Both the models had similar covariates, except slope and ruggedness. Since both these variables are highly correlated, we chose to use only the top model for the inferences. The final model showed density to be positively related to protection status, elevation and winter season (Table 3). A weak positive effect of slope was also found on the density (beta=0.056 SE 0.26). Maximum likelihood estimates of the real scale parameters with associated standard error are mentioned in Table 4. hood estimates of the real scale parameters with associated 95% confidence interval are mentioned in Table 4. Encounter rate varied with sex (β (male): 0.523 SE

Encounter rate varied with sex (beta (male): 0.523 SE 0.16) and camera trapping effort (beta: 0.011 SE 0.01). Space use was found to vary across sessions and sex. Snow leopard densities in the landscape varied from 0.03 individuals / 100 km^2 to 6.9 individuals / 100 km^2 (Fig. 2). Mean density was found to be 1.42 (SE 0.02) individual /100 km^2 in summer and 2.15 (SE 0.03) in winter inside the PA (Fig. 2, Fig.3). The mean density outside PA was 0.4 (SE 0.01) in summer and 0.6 (SE 0.01) in winter. The sex ratio was skewed towards females (Ψ (prob[male]): -1.194 SE 0.232). In terms of spatial scale parameter (σ), estimated space use was larger for males (0.23 SE 0.06) than females. Density-weighted connectivity showed that Gangotri National Park had a high density of snow leopards and is connected with PAs on western and south eastern side. On the western side, Kiyarkoti, Gidara, Siyaghad and Chorghad valleys provide connectivity with Govind National Park. On the south eastern side, Srikant valley provides the most conducive areas to connect with Kedarnath Wildlife Sanctuary (Fig.4 b, c).

Camera trap data was also used to compare the relative abundance (photo-capture rates: #/ 100 trap nights) of humans, livestock inside and outside PA. The mean photo-capture rate of humans in summer inside PA was: 58.12 SE 20.19 and 19.91 SE 6.53 outside the PA. In winters, mean photo-capture rate of humans inside PA was 5.01 SE 0.98 and was 7.28 SE 2.7 outside PA. For livestock (present only in summers) mean capture rate was 14.44 SE 3.47 and 12.46 SE 4.7 inside and outside PA respectively. Capture rate of prey species inside and outside PA are given as Supplementary Table 2.

Discussion

Conservation of large carnivores such as snow leopard goes beyond PAs and follows a large landscape approach that requires integration into human-dominated landscapes (Johansson *et al.* 2016). The feasibility of this approach depends on the ability of species to live in human-modified landscapes. We assessed the spatial density patterns of snow leopard along the gradient of anthropogenic pressures to understand the extent to which snow leopard can persist in human-modified areas. Additionally, delineating and protecting areas crucial for connectivity and dispersal among core protected areas is vital (Boron *et al*. 2016). Our study demonstrated how ecological distance SCR models could estimate spatially explicit densities of snow leopards and understand their movement in a multi-use landscape.

The spatial analysis of snow leopard density showed a higher density at high elevation alpine habitats in the landscape. Snow leopard density did not show significant variation among sessions and was therefore considered stable across the four monitoring years. Our results supported our hypothesis that densities differ across the landscape based on protection status and topography (slope and ruggedness). Snow leopard's preference for steep terrain (>40-50° slopes) is well emphasized in many previous studies. Similar finding from previous research suggest that rugged terrain and steep slopes are ideal sites for marking, resting, hunting, and escape cover (Jackson & Ahlborn, 1989; Chundawat, 1990, Jackson, 1996; Fox & Chundawat, 2016).

Distance from human settlement did not appear to significantly influence snow leopard density. The study area has few human settlements, all situated below the tree line. Livestock in these villages stay in alpine areas during summer and in low elevation (<1000 m) in winters. Villagers depend on tourism, agriculture, and horticulture practices for sustenance and thus have little impact on snow leopards. Reduction in human activities and absence of livestock in winter had a positive effect on snow leopard density. Earlier studies from this area have shown a similar negative response of snow leopards to the presence of livestock in summer (Pal *et al.* 2020). The detection probability of males was higher than females, most likely because of their different ranging patterns. Males are known to utilize more extensive home ranges than females (Johansson *et al.* 2016) and are likely to be captured more than females (Sollmann *et al.* 2011).

Using ecological distance formulation of the SCR model (Royle *et al.* 2013; Sutherland *et al.* 2015), we could account for spatial asymmetry in expected encounter probabilities around an activity center, which was found to be explicitly related to the less steep slopes. High ridges, deep gorges, peaks with rocky prominence, and craggy glaciers characterize the area. For example, Gangotri and Nelang valleys are divided by peaks such as Chaturbhij (6655 m), Mana group of peaks (6791-6771 m), and Bhagirathi group of peaks (6856 to 6454 m). Similarly, other major valleys such as Gangotri-Kedar Tal, Rudragyra-Srikant, and Kedar Tal-Rudragyra, are bifurcated by some of the highest peaks of Himalayan range (Pusalkar & Singh 2012). Given the strongly precipitous terrain, it is not surprising that snow leopards prefer low slope areas such as river valleys for movement. Both telemetry and sign surveys in other areas indicate that snow leopards strongly prefer to move along prominent terrain features such as bluff edges, gullies, or the base of broken cliffs (Jackson & Ahlborn 1989; Fox & Chundawat 1988). Such areas become even more critical during winters when most of the high reaches are covered in deep snow.

It is worth noting that, due to camera theft the number of cameras outside PAs was lower than inside (range across seasons: 4 (session 2) vs. 17 (session 6 and 7), respectively (table 1, Supplementary information 1). This could have led to lower captures of snow leopard outside PA.

However, the intensity of camera traps varied across the sessions, and an increase in camera intensity did not result in more captures. Hence, the low captures of snow leopards outside PA were most likely caused by the low density of snow leopard.

High human presence was found throughout the landscape, including PA. Besides grazing and tourism, the areas inside PA are under pressure from the paramilitary camp presence, road expansion, and other developmental activities (Chandola, 2008; Bhardwaj et al. 2010; Pal et al. 2020). The photo-capture rates also suggest higher presence of humans inside the PA than outside both in the summer and winter season. Despite this, snow leopard density was found higher inside the PA than outside PA (Fig. 2, Fig. 3). There is a difference in law enforcement and active space use regulation between protected and unprotected areas, which seems to have a positive effect on snow leopard density. The forest department and paramilitary forces actively patrol the areas inside the park. A limited number of tourists (~ 150) are allowed to visit Gangotri valley per day, and movement beyond 500 m of trails are restricted inside the park. Forest department checkpoints at the entrance of all the major valleys inside the park further help regulate human presence and prevent illegal activities. However such strict regulations are absent outside the park. Evidence of hunting was also found outside PAs as presence of snares (6 observations).

Another noticeable difference is the higher relative abundance of main prey of snow leopard inside the PA than outside (Pal *et al.* 2020). Bharal is the major contributor to the diet (frequency of occurrence: 29%, CI: 18-42; N= 54, Pal R, unpublished data) of snow leopards in the landscape. In summer, bharal capture rate was higher inside PA, compared to outside PA (Supplementary Table 1**)**. In winter, in the absence of livestock, there was a slight increase in the capture rate of bharal outside PA but was still less compared to the capture rate inside the PA (Supplementary Table 1**)**. Outside PA, wild prey suffers from both poaching and livestock grazing pressure. Diet analysis of snow leopards from the area also recorded a high presence of livestock (frequency of occurrence: 33 %, CI: 20-47; Pal R, unpublished data). At present, there are no reliable records of the conflict situation between snow leopards and nomadic pastoralists in the region. Compensation schemes by the forest department are available for livestock losses (outside PA) but are rarely reported by the nomadic pastoralists and were mostly reported by local villagers (WII 2021). No cases of snow leopard depredation on livestock were found in the official records of the past nine years (WII 2021). Most of the depredation reports were of common leopard and Asiatic black bear *Ursus thibetanus* from the village areas. This suggests that the nomadic pastoralists do not report livestock losses to snow leopards. Depredation could escalate into conflicts (Rashid *et al.* 2020) and lead to the retaliatory killing of snow leopard (Suryawanshi *et al.* 2013). There is an immediate need to understand the interaction between nomadic pastoralists and snow leopards, and herders' response to livestock depredation incidents.

Cost surface (Fig. 4a) showed that areas outside PA such as Kiyarkoti, Siyaghad, Chorgadh, and Gidara valleys provide the most conducive pathways for connecting the landscape with Govind Pasu Vihar National Park. The continuous chain of high peaks on the western side, for example, Chuakhamba (7138 m), Shivling (6543 m), Thalaysagar (6904 m), Jogin-I (6465 m), may limit direct connectivity of high-density areas (Gangotri valley, Kedar Tal) with Kedarnath Wildlife Sanctuary. Adjacent Srikant valley (outside PA), provides the most conducive pathway for connecting population of these two PAs (Fig.1; Fig.4 b,c). Except for Chorghad valley, DWC (Fig.1; Fig.4 b,c) showed relatively less use (low density) of all the potential corridors. Issues such as low prey availability, and hunting pressure may need to be resolved to make these corridors functionally conducive to snow leopard movement. Studies have shown that avoidance of human-related risks and low prey availability can strongly constrain the functional connectivity for carnivores (Ghoddousi *et al.* 2021).

Snow leopard density (individual/ km^2) inside Gangotri National Park (summer: 1.42 SE 0.02/100 km^2; winter: 2.15 SE 0.03), was lower than Khangchendzonga, Sikkim (Sathyakumar *et al.* 2013: 4.1 SE 1.81), and Qilianshan, China (Alexander *et al.* 2015: 3.35 SE 1.01) and was higher than most of other earlier studies (Alexander *et al.* 2016: 1.40 SE 0.36, Kachel *et al.* 2017: 0.4 SE 0.20, Chetri *et al.* 2019: 0.95 SE 0.19; Sharma *et al*. 2021: 0.5, 95% CI: 0.31–0.82). Camera trapping effort confirmed the presence of a minimum of nine breeding females inside the PA. Of these, one particular female gave birth at least twice in four years (2015, 2019), suggesting an active breeding population inside the PA.

Our study confirms the presence of high density of snow leopards, an active breeding population, and connectivity with other suitable habitats, hence establishing Gangotri National Park as a strategically crucial source population for snow leopard conservation in the landscape. Areas outside PA such as Srikant, Chorghad, Kiyarkoti and Siyaghad are important for maintaining continuity between Gangotri and adjacent PAs. The high density of snow leopards inside PA despite the presence of a range of human activities indicates the importance of protection in sustaining the snow leopards alongside multiple human use practices. Low density outside PA requires management attention especially the areas identified as potential corridors for snow leopards to maintain connectivity. We recommend developing pockets of livestock-free areas accompanied by awareness programs, effective compensation schemes, and local communities' support (Mishra *et al.* 2017; Koete *et al.* 2021) to revive the prey base outside PA (Mishra *et al.* 2016). As of now, very little information exists on the interaction of snow leopards and nomadic pastoralists in the region. Since nomadic pastoralists are the main stakeholders of snow leopard habitats, conservation practitioners need to work closely with them (Schwerdtner & Gruber, 2007).

The approach used in this study is an efficient way to quantify the relationship between landscape characteristics and species movement based on encounter history data and provides realistic spatially explicit connectivity estimation. Most of the connectivity modeling approaches currently in use are based on predicting connectivity across a resistance surface based on expert opinions. These methods lack formal estimation of biological responses of the focal species to landscape characteristics using data collected in the field. However, landscape connectivity is often species-specific (Goodwin, 2003), and mapping reliable connectivity requires parameterization based on empirical movement data in response to landscape characteristics. This is often challenging due to the high cost of generating sufficient movement data of dispersing individuals or genetic structures across landscapes. SCR is a widely used tool for estimating densities of a wide range of species (Sollmann *et al*. 2011, Harihar *et al.* 2020). The ecological modeling approach is an analytical step forward from the conventional SCR approach to jointly estimate density and landscape connectivity of species, providing information about critical conservation areas.

A land sparing strategy, relying on PAs alone, is inadequate for the long-term conservation of large carnivores (Johansson et al. 2016). They have to be integrated within a matrix of human-modified areas into wider connected landscapes. Our study provides some crucial insights into carnivore conservation in a human-dominated landscape. Firstly, effective regulation of human behavior and resource use is the key to the survival of carnivores in a multi-use landscape. Co-coordinating the efforts of researchers, communities, managers, and policy leaders are critical for attaining success. Accomplishing carnivore conservation across vast multi-use landscapes is possible, as exemplified by the recovery of large carnivore populations which was mainly enabled by public support, legislation, and law enforcement (Linnell *et al.* 2001, Jhala *et al.* 2020). Secondly, conservation in human dominated landscapes relies primarily on connectivity between landscapes shared with humans and core areas for breeders (Rio-Maior *et al*. 2019). Avoidance of human risk and unavailability of prey can constraint dispersal opportunities (Ghoddousi *et al*. 2021). Our study suggests that although snow leopard is tolerant towards direct human presence and habitat modification, potential conflict with herders and prey depletion may limits its use of critical areas facilitating connectivity. Therefore, for a successful coexistence model, along with the identification of suitable habitats, conservation practices need to moderate human activities and require integrated management approaches to ensure landscape-scale connectivity.

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Table 1 Summary of sampling effort for seven seasonal camera trap sessions (2015–2019), conducted in Gangotri landscape : the year of the survey, season, number of camera stations, number of trap nights, number of independent snow leopard photographs (multiple captures of the same individual within 24 hours at a camera site were excluded), number of unique adult individuals detected per survey, average captures (average of the number of times captured individuals were detected) and average spatial captures (average of the number of unique cameras captured individuals were detected at).

Session	Year	Season	No. of camera stations	No. of trap nights	No. of independent photographs	No. of unique individuals	Average captures	Average spatial captures
1	2015-16	Winter (Nov to March)	50	5,750	225	25	11.04	3.00
2	2016	Summer(May to September)	46	4,652	32	13	2.62	1.62
3	2016-17	Winter(Nov-March)	44	3,420	93	15	6.87	2.40
4	2017	Summer(May to September)	101	9,868	44	12	3.67	2.42
5	2017-18	Winter (Nov to March)	100	10,100	175	23	8.39	3.57
6	2018	Summer(May to September)	89	8,173	64	18	3.61	2.22
7	2018-19	Winter (Nov to March)	82	7,223	80	24	3.62	1.96

Table 2 Description of the effect used to explain the variation in the spatial capture recapture model components.

Category	**Variable**	**Hypothetical effect**	**Citation**	**Source**
Density	Session	Density different across all the sessions	Farhadinia et al., 2021	
	Season	Density different in summer and winter	Dul'a et al., 2021	
	Elevation	Density increases with increase in elevation	Khanal et al., 2020 Alexander et al., 2016b	Shuttle Radar Topography Mission (Jarvis et al., 2008).
	Ruggedness	Density increases with increase in ruggedness	Khanal et al., 2020 Sharma et al., 2021	Ruggedness raster was created using terrain analysis tool in QGIS from Elevation layer
	Distance to human settlement	Density increases with increase in distance from human habitation	Khanal et al., 2020 Alexander et al., 2016b	Euclidean distance raster created in ArcGis based on shape file of human settlements downloaded from Socioeconomic Data and Applications Center (Meiyappan et al., 2018)
	NDVI	Density increases with decrease in NDVI (alpine habitats)	Forrest et al., 2012	MODIS (Didan, 2015)
	Slope	Density increases with increase in slope	Chundawat, 1990; Fox & Chundawat, 2016	Slope raster was created using spatial analyst tool in ArcGis *10.4* software from Elevation layer
	Status	Density higher inside protected area	Rosenblatt et al., 2016	
Detection	Sex	Detection varies among male and female	Sollmann et al., 2011; Johansson et al., 2016	
	Effort	Detection increases with more trapping effort		
Sigma (rate at which detection probability declines as a function of distance)	Constant	Space use is constant across all the sessions		
	Session	Space use is different across all the sessions		
	Sex	Space use varies by sex	Johansson et al., 2016	
Movement	Euclidean distance	Uniform movement		
	Slope	Movement depend upon slope	Chundawat, 1990; Fox & Chundawat, 2016	
	Ruggedness	Movement depend upon ruggedness	Chundawat, 1990; Fox & Chundawat, 2016	

Table 3 Top five candidate models for evaluating the role of covariates on Density (*D*), detection probability (*p*), spatial scale (*σ*) and ecological distance (asu).

S.No	**Model**	**K**	**AIC**	**ΔAIC**	***wi***	***Σwi***
1	***D***(~season + status + slope + elevation) ***p***(~sex + effort) σ (~session + sex) asu(~slope - 1)	18	3191	0.0	0.39	0.39
2	***D***(~season + status + ruggedness + elevation) ***p***(~sex + effort) ***σ*** (~session + sex) asu(~slope - 1)	18	3191	0.028	0.38	0.77
3	***D***(~status + slope + elevation) ***p***(~sex + effort) ***σ*** (~session + sex) asu(~slope - 1)	17	3193	2.64	0.1	0.88
4	***D***(~ season + elevation) ***p***(~sex + effort) ***σ*** (~session + sex) asu(~slope - 1)	16	3194	3.71	0.061	0.94
5	***D***(~status + season+ slope + ndvi) ***p***(~sex + effort) ***σ*** (~session + sex) asu(~slope - 1)	18	3196	5.317	0.027	0.96

Note: In the table, K is number of parameters , AIC is Akaike Information Criteria, ΔAIC is difference between AIC of each model and the model with the lowest AIC, *wi* is AICc weights and *Σwi* is cumulative AIC weights.

Table 4 Maximum likelihood estimates (MLE) and standard error (SE) of estimated parameters for AIC-top model (*D*(~season + status + slope + elevation) *p*(~sex + effort)) *σ* (~session + sex) asu(~slope - 1) and the inferred sex ratio (*Ψ*).

	Parameters	**Estimate**	**S.E**
Detection	Intercept	-0.22	0.185
	Male	0.523	0.162
	Effort	0.011	0.001
Sigma	Intercept	-0.276	0.135
	Male	0.227	0.059
	Session 2	-0.199	0.1
	Session 3	-0.239	0.092
	Session 4	0.011	0.07
	Session 5	0.12	0.06
	Session 6	-0.26	0.077
	Session 7	-0.262	0.105
Density	Intercept	-4.069	0.338
	Intercept: winter	0.418	0.193
	Intercept: Protected area	0.66	0.289
	Slope	0.056	0.262
	Elevation	0.838	0.298
Movement cost	Slope	-0.52	0.043
Ψ(prob[male])		-1.194	0.232

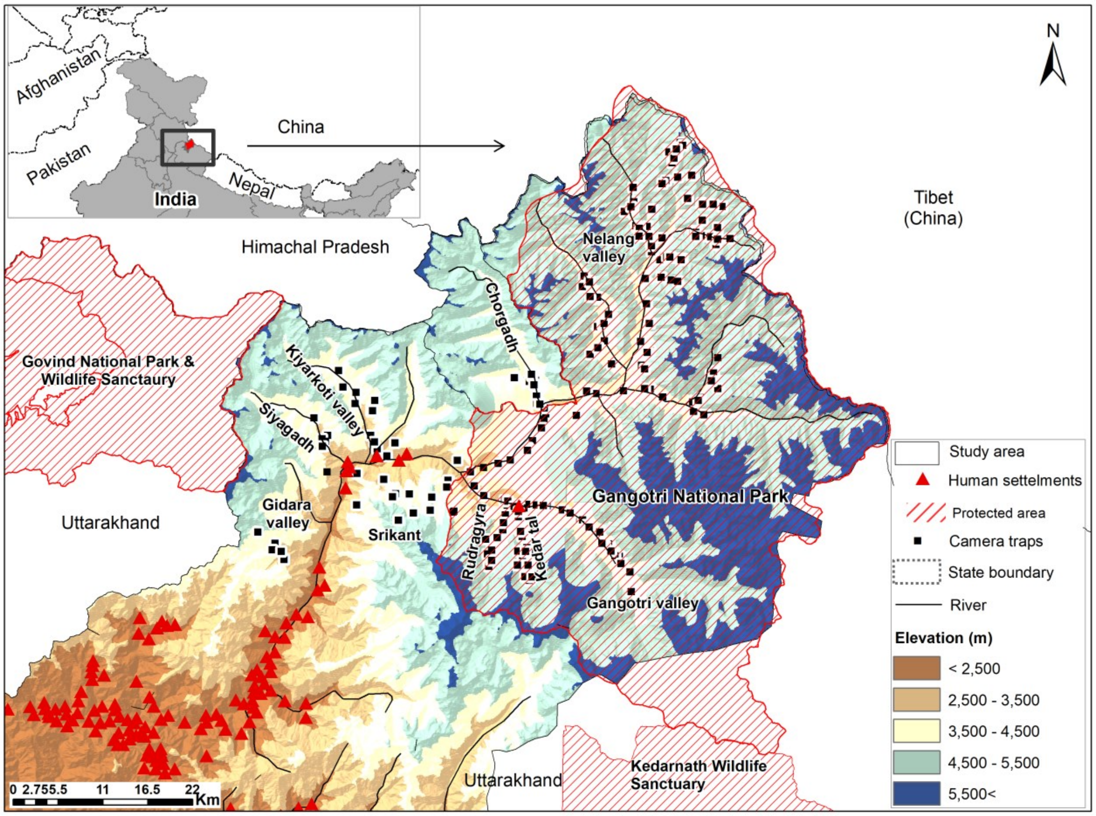


Fig. 1. Study area with location of camera traps. The inset map shows the location of the study area, Gangotri landscape in Uttarakhand state, Western Himalaya, India.

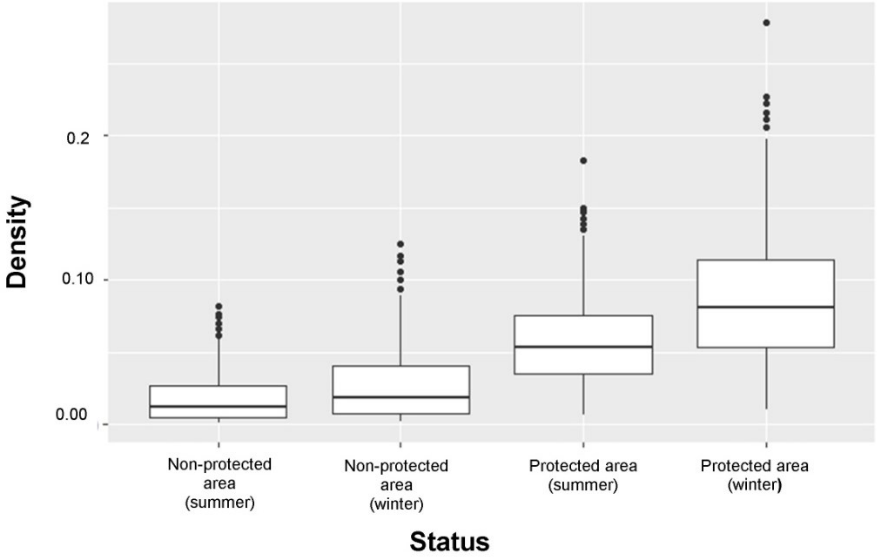


Fig. 2. Density (/ 4 km^2) of snow leopard in summer and winter inside protected and outside protected area in Gangotri landscape.

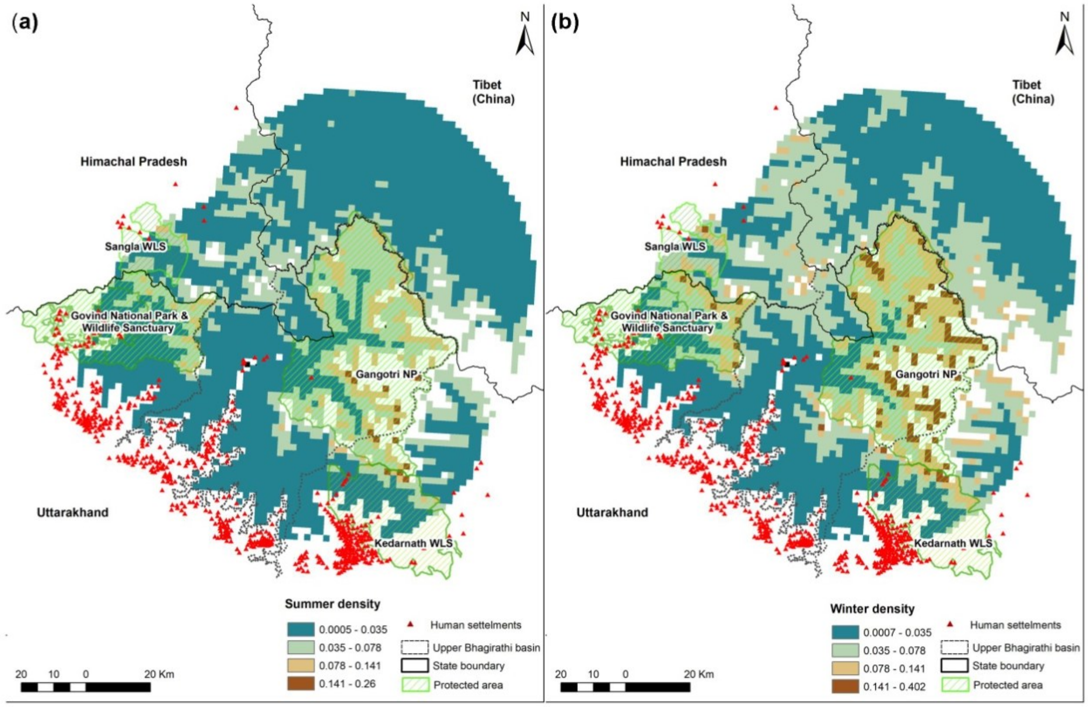


Fig. 3. Snow leopard density (/ 4 km^2) in summer (a) and winter (b) in Gangotri landscape and buffer areas based on estimates of the best SCR model derived from the camera-trap sampling.

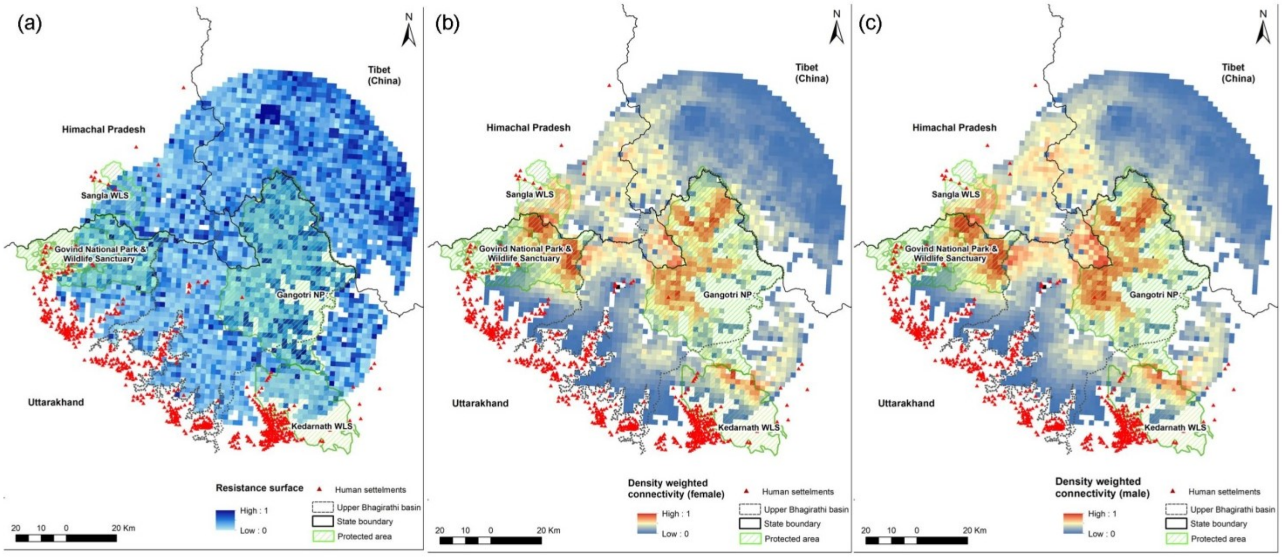
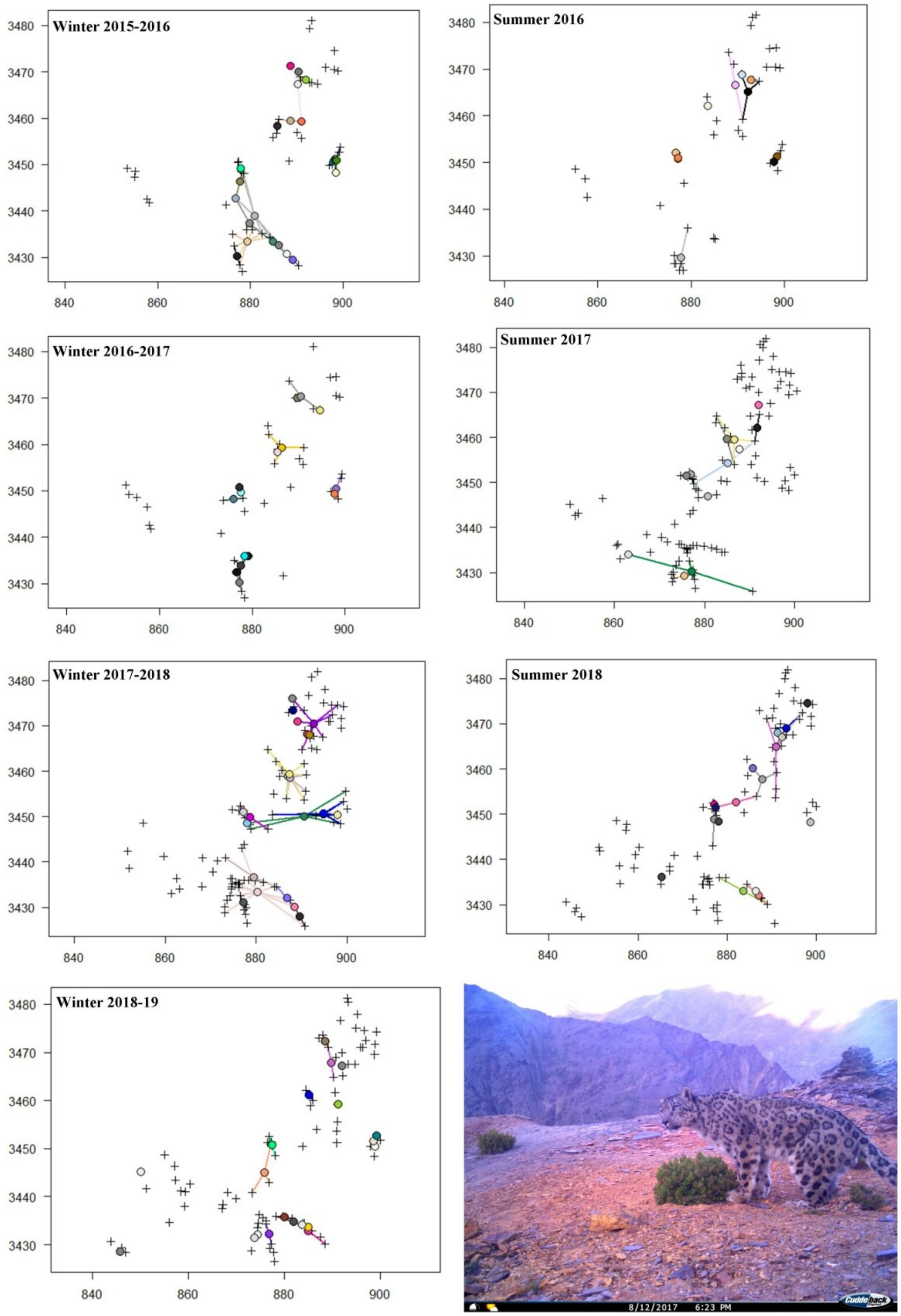


Fig. 4. Connectivity between different valleys for snow leopard in Gangotri landscape and buffer areas based on best supported ecological distance spatial recapture model: (a) Resistance surface (b) Density weighted connectivity for females (c) Density weighted connectivity for males

Supplementary Information



Supplementary Figure 1: Visualization of the spatial capture recapture from the seven sessions. Crosses (+) show the trap locations. Each filled circle represents the spatial average of all detection of a unique individual. Lines join average locations at the traps in individuals were captured (each point and line color represents a unique individual). Circles without lines are individuals that were detected at only a single location.

Supplementary Table 1: seasonal capture rate ± standard error (#/ 100 trap nights) of potential large and medium size prey of snow leopard inside and outside protected area, Upper Bhagirathi basin.

	Summer		**Winter**	
Species	**Protected area**	**Outside protected area**	**Protected area**	**Outside protected area**
Bharal *Pseudois nayaur*	3.57±1.06	0.23±0.12	3.47±0.53	1.67±0.7
Himalayan tahr *Hemitragus jemlahicus*	0.019±0.01	0.67±0.49	0.035±0.025	1.18±0.61
Musk deer *Moschus spp.*	0.5±0.3	1.54±0.73	0.33±0.11	2.57±1.14
Goral *Naemorhedus goral*	0.09± 0.06	0.31±0.17	0.12±0.085	0.97±0.48
Himalayan serow *Capricornis thar*	--	0.82±0.38	--	0.199±0.12
Sambar *Rusa unicolor*	--	0.45±0.25	--	0.67±0.61
Argali *Ovis ammon*	4*			
Himalayan Marmot *Marmota himalayana*	0.44±0.28	--	--	--
Tibetan woolly hare *Lepus oiostolus*	2.52±0.69	--	2.18±0.63	--
Himalayan langur *Semnopithecus entellus*	0.06±0.05	1.47±0.4	0.18±0.064	1.32±0.46
Rhesus macaque *Macaca mulatta*	0.18±0.1	0.23±0.21	0.04±0.026	0.009±0.01