Received: 18 February 2021 | Accepted: 26 October 2021

DOI: 10.1002/2688-8319.12115

Ecological Solutions and Evidence
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Estimating snow leopard and prey populations at large spatial scales

Kulbhushansingh Suryawanshi[1,2,5] | Abinand Reddy[1] | Manvi Sharma[1] | Munib Khanyari[1,3,4] | Ajay Bijoor[1,2] | Devika Rathore[1] | Harman Jaggi[1] | Abhirup Khara[1] | Aditya Malgaonkar[1] | Abhishek Ghoshal[1] | Jenis Patel[1] | Charudutt Mishra[1,2]

[1] Nature Conservation Foundation, Mysuru, India

[2] Snow Leopard Trust, Seattle, Washington, USA

[3] Interdisciplinary Center for Conservation Sciences, University of Oxford, Oxford, UK

[4] School of Biological Sciences, University of Bristol, Bristol, UK

[5] Wissenschaftskolleg zu Berlin, Berlin, Germany

Correspondence
Manvi Sharma, Nature Conservation Foundation, 1311, 12th Main, Vijayanagar 1st Stage, Mysore 570017, India.
Email: manvigsharma@gmail.com

Funding information
Himachal Pradesh Forest Department; Cholamandalam Investment and Finance Company Limited; National Geographic Society, Grant/Award Number: ww-067es-17; British Ecological Society, Grant/Award Number: LRB17\1004; Disney Conservation Fund

Handling Editor: Chloe Sato

Abstract

1. Effective management of charismatic large carnivores requires robust monitoring of their population at local, regional and global scales. While enormous progress has been made to estimate carnivore populations at local scales, estimates at regional and global scales remain elusive. In the first systematic effort at a large regional scale, we estimated the population of the elusive snow leopard *Panthera uncia* over an area of 26,112 km^2 in the Indian state of Himachal Pradesh.
2. We stratified the entire snow leopard habitat in Himachal Pradesh based on an occupancy survey. Subsequently, we conducted camera trapping surveys at 10 sites distributed proportionately, that is with similar coverage probability across the three strata. We conducted simulations to understand how unidentified captures could affect our model estimate. We also assessed populations of the primary wild ungulate prey of snow leopards – blue sheep *Pseudois nayaur* and Siberian ibex *Capra sibirica*.
3. Our results yielded a mean estimated density of 0.19 (95% confidence interval [CI]: 0.12–0.31) snow leopards per 100 km^2 and population size of 51 (95% CI: 34–73) snow leopards in Himachal Pradesh. The density estimates for individual sites ranged from 0.08 to 0.37 snow leopards per 100 km^2. Simulations showed that unidentified snow leopard captures did not seem to affect the accuracy of our model estimate but could have affected the precision. Wild ungulate prey density ranged from 0.11 to 1.09 per km^2. Snow leopard density showed a positive linear relationship with prey density (slope = 0.25, $SE = 0.08$, $P = 0.01$, $R^2 = 0.51$).
4. Our study shows the earlier opinion-based estimate for Himachal Pradesh to have been significantly positively biased. Using occupancy surveys to stratify large areas in order to design camera trap surveys addresses one of the common spatial sampling biases, that is limited sampling of only prime snow leopard

habitats. Our work validates two-step approach recommended in the ongoing initiative of the 12 snow leopard range countries for Population Assessment of World's Snow leopards (PAWS program), and cautions against the use of opinion-based estimates for assessing the status of species of critical conservation importance.

KEYWORDS
camera trap, density estimation, India, *Panthera uncia*, population size, Spatially Explicit Capture–Recapture, ungulate prey density

1 | INTRODUCTION

Range-wide population estimates for species of global conservation concern are necessary for effective conservation planning, priority setting and monitoring the impact of conservation efforts. It is especially important for charismatic species that represent entire ecosystems because of the public interest they generate. Large carnivores such as the tiger *Panthera tigris*, lion *Panthera leo*, jaguar *Panthera onca* and snow leopard *Panthera uncia* are often used as flagship species or umbrella species to raise support for the conservation of their habitats and associated species (Caro, 2010). However, some of the traits of these species that make them suitable surrogate species (large home range sizes, low density, secretive behaviour that elicits public interest) also make it difficult to monitor them through statistically robust population estimation techniques (Karanth, 1995).

Technological developments in camera traps and molecular genetics, together with advancement of statistical tools to model for imperfect detection, have improved the ability to estimate populations of large carnivores in any given site (Borchers & Efford, 2008; Efford et al., 2009; Karanth, 1995). However, scaling these efforts to obtain regional or global estimates is cost and effort intensive, and unfeasible for many species. In the absence of global estimates, conservation assessments such as IUCN Red List of Threatened Species rely on information derived from a few sites (typically protected areas) in combination with 'expert' opinions (Ale & Mishra, 2018). Opinions, however, are subjective, laden with unaccounted uncertainty and often founded on incorrect or outdated assumptions (Akcakaya et al., 2000). Unless planned appropriately with necessary stratification and conducted over large enough areas, population estimates from a few sites are often not representative of the larger distribution of the species and can lead to biased regional or global estimates (Suryawanshi et al., 2019).

The snow leopard is a flagship species for the high mountains of South and Central Asia and occurs in 12 countries (McCarthy et al., 2017). These mountains are considered the water tower for a third of humanity, most of which lives downstream in the river valleys and plains (Immerzeel et al., 2010). Habitat degradation and fragmentation due to large infrastructure projects, depletion of wild prey populations, persecution over livestock predation, poaching and illegal wildlife trade are some of the most important threats to the snow leopards (Ale & Mishra, 2018; Li et al., 2020). Snow leopards are known to range widely and hence their conservation requires efforts on land well beyond protected area boundaries to promote coexistence with local communities (Ale & Mishra, 2018; Johansson et al., 2016). Currently, a reliable global population estimate for snow leopards is unavailable. It has been suggested that there could be around 3900–8745 snow leopards globally, but these numbers are largely based on opinions (McCarthy et al., 2016). Using such opinion-based estimates, snow leopards were downlisted in the IUCN Red List of Threatened Species from Endangered to Vulnerable in 2017, assuming that the snow leopard populations meet the condition that there were more snow leopards than previously thought (McCarthy et al., 2017). However, this change was opposed by many country governments and scientists as relying largely on opinions and not on scientific data (Ale & Mishra, 2018; GSLEP Secretariat, 2017).

Robust methods of estimating snow leopard population size require adequate sample counts based on camera trap (Karanth, 1995) or molecular genetics (Mondal et al., 2009). Both these methods have become popular especially following their widespread adoption in monitoring tiger populations (Jhala et al., 2019; Karanth et al., 2004). The cameras are placed in micro-habitats preferred by snow leopards but spread across the study area in a uniform grid system or distributed based on a randomized spatial design (Alexander et al., 2015; Jackson et al., 2006; Sharma et al., 2014). Individual snow leopards are identified from photographs using individually distinct fur patterns and the data are analysed by creating individual capture histories to estimate density and population size (Alexander et al., 2015; Sharma et al., 2014).

Even with the use of camera traps, inadequate sampling or errors in data have been shown to lead to overestimation in population abundance. Camera trap-based methods, for example, assume that individual snow leopards can be identified accurately from camera trap photographs. However, Johansson et al. (2020) found that even experienced observers made significant mistakes in identification of snow leopards from photographs, leading to consistent overestimation of populations. They reported that observers on average misclassified 12.5% of the capture occasions, generating up to 31% erroneous 'ghost' individuals, leading to an average of 35% inflation in the abundance estimate when using capture–recapture estimation methods (Johansson et al., 2020). Similar possibility of misidentification of

individuals also exists in the genetic analysis of snow leopard scats (Janečka et al., 2008). Suryawanshi et al. (2019) further identified two important sources of bias in existing studies of snow leopard abundance: (i) relatively small study areas which leads to overestimation of the snow leopard population in the study site (Suryawanshi et al., 2019), and (ii) preferential sampling of prime snow leopard habitats, often in well-protected sites, which leads to inflated density if extrapolated to larger landscapes.

Following the change in Red List status of snow leopards, the governments of all 12 snow leopard range countries (Afghanistan, Bhutan, China, India, Kazakhstan, Kyrgyzstan, Mongolia, Nepal, Pakistan, Russia, Tajikistan and Uzbekistan) initiated a collaborative effort called PAWS, or Population Assessment of World's Snow Leopards, to arrive at robust national and global estimates of snow leopards in the wild (GSLEP Secretariat, 2017). Recognizing the existing and potential sampling biases, the Technical Advisory Committee of PAWS recommended a two-step sampling protocol – (i) site occupancy modelling over relatively large areas based on sign or interview surveys, and (ii) stratified sampling for population abundance through camera traps or genetics ensuring adequate coverage of habitat heterogeneity (Sharma et al., 2019).

Here, we present the results of the first attempt to arrive at a robust estimate of snow leopard abundance at a regional scale employing a stratified design. We assessed snow leopard abundance in a large landscape of over 26,112 km^2 comprising the entire snow leopard habitat in the state of Himachal Pradesh in India (Figure 1). The size of our study area was one and half times the size of the entire area covered cumulatively by all published snow leopard population estimation studies conducted so far across its range (Chetri et al. 2019; Khanal et al., 2020; Suryawanshi et al., 2019). The primary goal of our study was to demonstrate a two-step sampling approach for estimating the population of snow leopards at a large spatial scale. We did this by conducting population assessments throughout the state of Himachal Pradesh. We employed a stratified study design using data from our earlier occupancy surveys (Ghoshal et al., 2019). Our study contributes towards a robust global population estimate of snow leopards, as well as generates methodological insights for the PAWS effort.

2 | MATERIALS AND METHODS

2.1 | Study site

Of the 55,673 km^2 area covered by the Indian state of Himachal Pradesh, approximately 26,000 km^2 area is potential snow leopard habitat, that is areas above the treeline, typically between 3000 and 6000 m elevation range, sometimes including areas below this elevation cut-off where the treeline is lower (Ghoshal et al., 2019; Snow leopard network, 2014). This potential habitat spans a contiguous area spread over the Trans- and Greater-Himalayan mountains (Figure 2a). Though snow leopards can venture into lower areas, the high elevation pastures, ridgelines and cliffs are their main habitats (Jackson, 1996). The two main prey species of the snow leopard in Himachal Pradesh – blue sheep *Pseudois nayaur* and ibex *Capra sibirica* – mostly occur in high altitude pastures and in relatively rugged terrain (Bagchi & Mishra, 2006). Other prey species of the snow leopard in parts of our study area included the Himalayan tahr *Hemitragus jemlahicus* and musk deer *Moschus* sp., both of which occur around the treeline.

2.2 | Study design

We estimated the density of snow leopards in the entire available habitat of Himachal Pradesh using a stratified sampling design. We used a two-step sampling process to ensure a robust design and proportionate coverage of the snow leopard habitat following the recommendation of the PAWS protocol (Sharma et al, 2019) that has been adapted by the Government of India (MoEFCC, 2019). All fieldwork was conducted after obtaining permissions from the Himachal Pradesh Forest Department.

In the first step, we stratified the entire potential snow leopard habitat in Himachal Pradesh based on data from a snow leopard occupancy survey conducted by Ghoshal et al. (2019). This study sampled 14,616 km^2 across 88 grid cells (15 × 15 km) which were spread over a study area of ~20,000 km^2 across three districts of Kinnaur, Lahaul–Spiti, and Chamba regions, covering over 75% of the potential snow leopard distribution in the state (areas above the treeline). Regions with occupancy probability greater than 0.75 were identified as high-occupancy stratum, regions with occupancy probability less than 0.75 were identified as low-occupancy stratum (Figure 2b) and potential snow leopard habitats that were not surveyed by Ghoshal et al. (2019) were categorized as the 'unknown' stratum. For details on stratification method, see Supporting Information 2.

Within each stratum, we conducted camera trapping at multiple snow leopard areas, henceforth referred to as sites. We sampled a total of 10 sites (Table 1): five in the high-occupancy stratum that together covered 12,724 km^2, three in the low-occupancy stratum that covered 8019 km^2 and two in the unknown stratum that covered 5369 km^2. Within each stratum, we considered the design requirements of Spatially Explicit Capture–Recapture (SECR), such as adequate camera density to enable multiple captures of individual snow leopards at different locations, and avoiding highly linear placement of cameras. We also considered the availability of at least 500 km^2 of continuous snow leopard habitat within the same watershed (valley) area following the recommendation of Suryawanshi et al (2019). Habitat patches that were smaller were assumed to have densities similar to the rest of the strata and were likely to be included in the buffer areas of the sampled sites (see Figure S3).

2.2.1 | Camera trapping

Camera trap surveys were conducted in early spring (April–May) or during autumn to early winter (October–December) from 2017 to 2019 (Table 1). We deployed 20–36 Reconyx HC500 camera traps in each site to ensure at least one camera trap per grid and at least two or

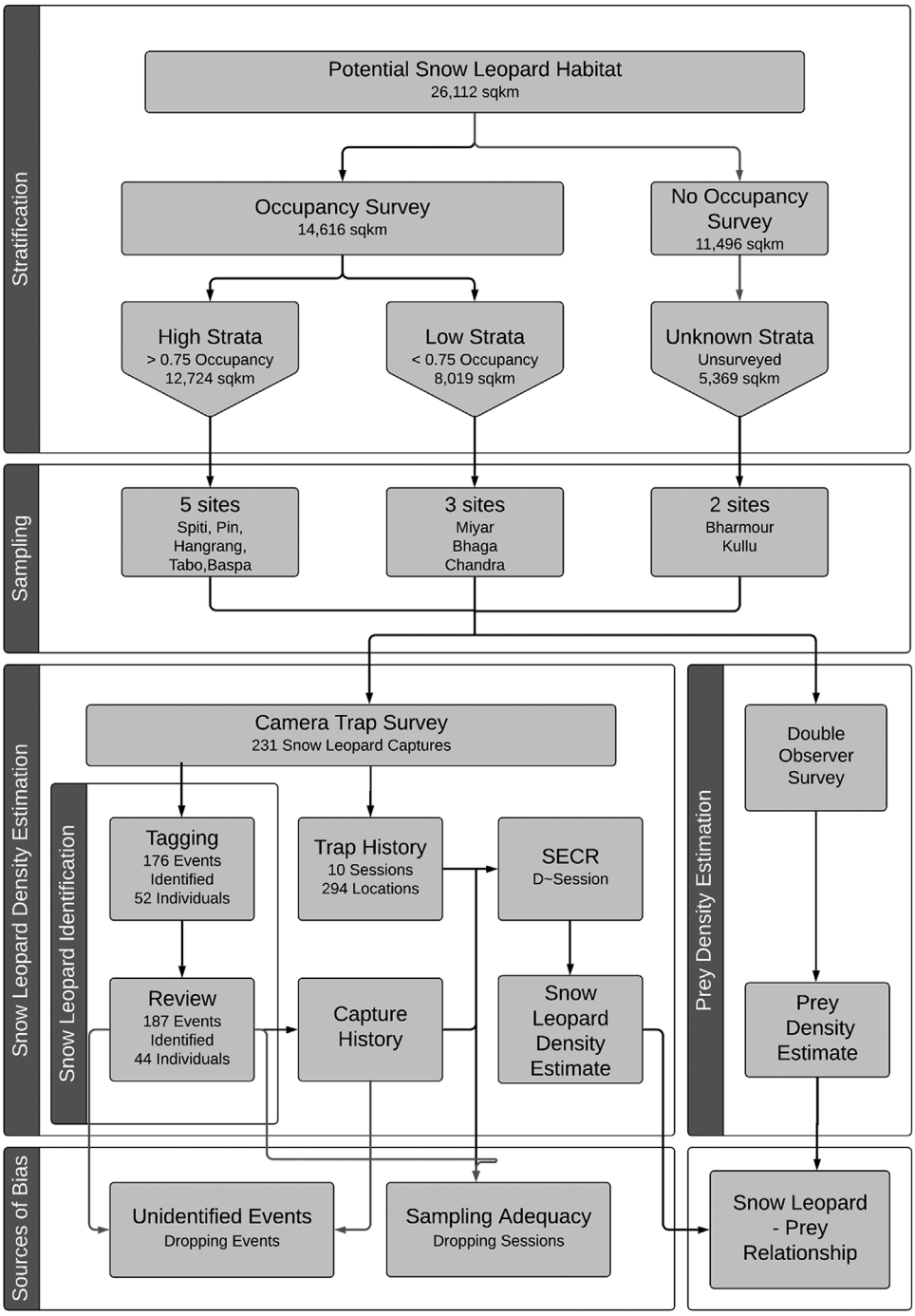

FIGURE 1 Conceptual representation of our study design and methods used to estimate the density of the snow leopard and its prey across a large landscape of 26,112 km^2 in the state of Himachal Pradesh, India. Spatially Explicit Capture–Recapture is abbreviated as SECR in the figure

more camera traps (Sollmann et al, 2012) within reported home range size estimates, that is 207 and 124 km^2 for male and female snow leopards, respectively (Johansson et al. (2016). The cameras were installed for 60 days, during which cameras were checked once for battery condition and for replacement of memory cards.

Each site was uniformly covered by deploying one camera in a 4 × 4 km systematic grid that has been used to estimate snow leopard densities (Alexander et al., 2015). It is smaller than the estimated home range size of snow leopards, thus allowing for the possibility of capture across multiple traps to allow for a robust estimation of the scale of movement in a spatially explicit analysis. We did not deploy camera traps in grids below the altitude of 2000 m, as they were far below the elevational limits of the snow leopard habitat. We also avoided grids in permafrost. Except for the inaccessible grid cells, at least one camera was deployed in each cell. Cameras were installed based on prevalence of snow leopard signs such as hair, scat, scrape or urine spray marks and suitable microhabitats to maximize detection within each cell. At one site (Kullu), due to the rugged landscape, instead of a uniform design,

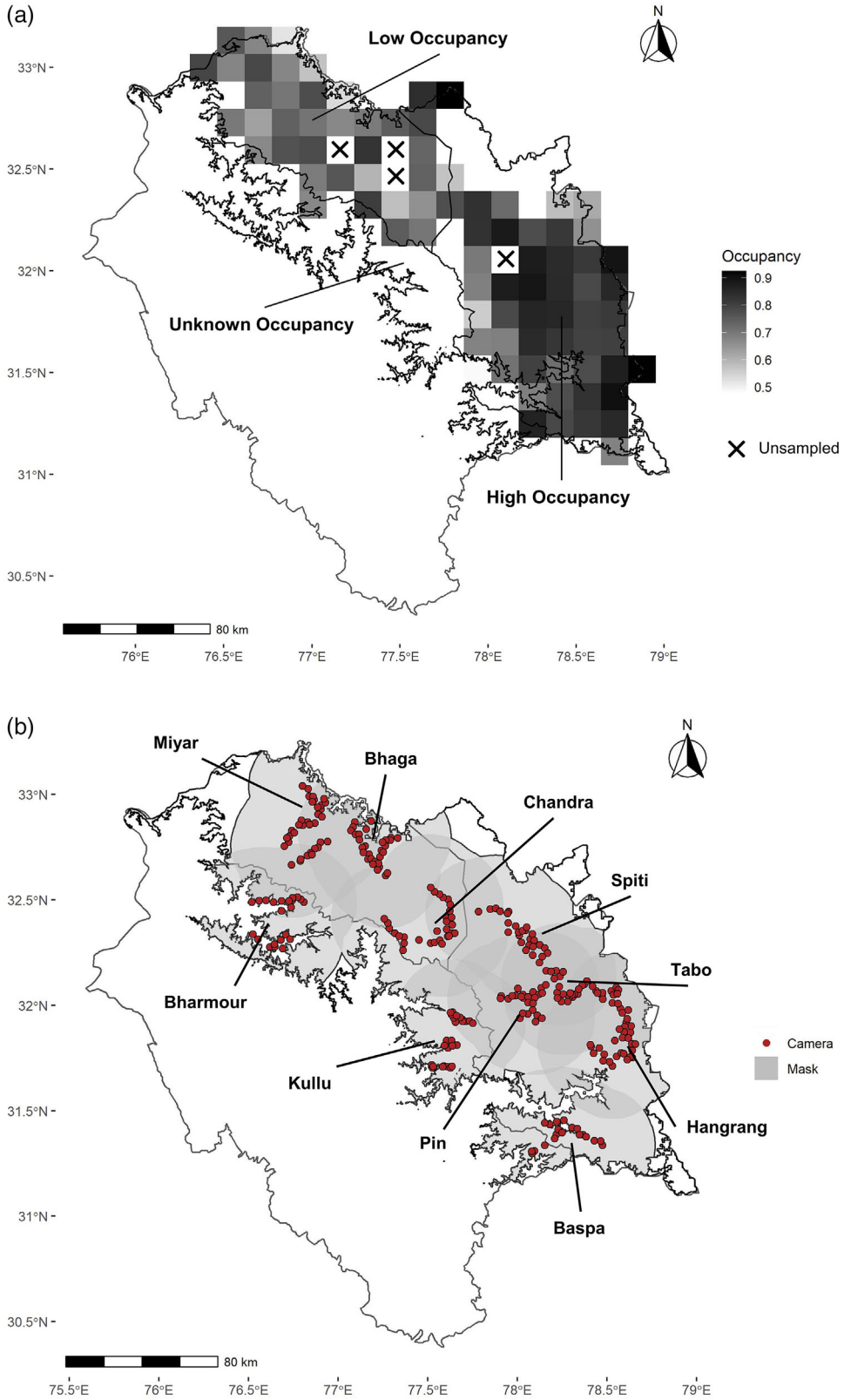

FIGURE 2 (a) The potential snow leopard habitat in Himachal Pradesh stratified into three regions based on snow leopard occupancy (Ghoshal et al., 2019). The regions marked with a cross represent grids with very high mountains and glaciers (>6000 m) that were not sampled. (b) Camera trapping sites (red dots) and the habitat mask (shaded region) covering the three strata – high: Spiti, Hangrang, Tabo, Pin and Baspa; low: Bhaga, Chandra and Miyar; unknown: Bharmour and Kullu

TABLE 1 Site wise details about camera trapping effort and results from 10 sampled sites in the Indian state of Himachal Pradesh. Estimated area is the number of 4 × 4 km grids with cameras times the area of the grid

Names of the site	Estimated area (km^2)	Number of camera traps deployed	Number of occasions (days)	Number of snow leopard detections	Number of individual snow leopards	Estimate snow leopard density per 100 km^2 (95% CI)
Bhaga	480	30	60	9	1	0.05 (0.01–0.24)
Bharmour	352	21	60	1	1	0.06 (0.01–0.31)
Chandra	496	31	60	18	3	0.1 (0.03–0.29)
Kullu	480	30	60	22	2	0.1 (0.03–0.35)
Miyar	576	36	60	5	2	0.07 (0.02–0.26)
Pin	370	25	60	19	6	0.27 (0.12–0.61)
Baspa	320	20	60	7	3	0.18 (0.06–0.51)
Tabo	464	29	60	27	9	0.37 (0.18–0.72)
Hangrang	484	31	60	18	8	0.36 (0.17–0.73)
Spiti	760	31	60	61	9	0.3 (0.15–0.59)

we had to deploy the camera traps in a clustered manner following the recommendations of Sharma et al (2019). Four cameras in the Baspa site, which was part of the high-occupancy stratum, had to be placed in the adjacent area belonging to the 'unknown' stratum due to inaccessibility. The northern and eastern parts of this site were highly inaccessible, whereas the southern areas falling in the 'unknown' stratum were continuous with our site and were assumed to have similar snow leopard density.

2.2.2 | Double-observer surveys for prey density estimation

We used double-observer surveys, which are based on mark–recapture theory, to estimate the density of the predominant wild prey species – Blue sheep and Ibex – in each of the 10 sites (Forsyth & Hickling, 1997; Suryawanshi et al., 2012; Suryawanshi et al., 2021). Although Himalayan tahr and musk deer were recorded in three and four sites, respectively, they were distributed close to the treeline in habitats typically used by the common leopard (*Panthera pardus*). These two species were excluded from the snow leopard prey population estimates. The total area sampled for wild ungulates across the 10 sites was 4489 km^2 (Table 2). We conducted double-observer surveys with both the observer teams walking each transect on foot. The total survey effort was 749 km that was surveyed twice. In the double-observer survey approach, the unit being 'marked' and 'recaptured' is the individual ungulate group rather than the individual animal (Forsyth & Hickling, 1997). For field data collection, each of the 10 sites was divided into smaller blocks based on landform and topological features for ease of survey. Each block was surveyed by two teams, with the second team starting their survey 15–30 min after the first team had started its survey (Suryawanshi et al., 2012). Each team searched for and independently counted the ungulate groups and the number of animals in each group. While doing so, they ensured not to cue the other team about their ungulate detections. Survey routes were chosen to allow for complete visual coverage of each block. The surveys involved three main assumptions: (1) entire visual coverage of each block was possible during the survey, (2) two individual teams, each containing similar number of surveyors, conducted the surveys and obtained detections independently of each other and (3) the ungulate groups could be identified individually based on the size and the age–sex composition of a herd, its location and any other peculiarities that the teams could note. The data collected included group size, species and age–sex composition. Detection or non-detection of each ungulate group by each observer team was noted post-survey. Eight observers were involved in the surveys at each site. Other details of the field methods can be found in Suryawanshi et al. (2012). Wild ungulate abundance estimation in each site was conducted in the same year as camera trapping for snow leopards in that site. Ungulate surveys in Spiti, Tabo, Pin and Hangrang were conducted in the month of May and in the other sites in October.

2.3 | Image tagging and snow leopard individual identification

A major source of bias in population assessments of snow leopards has been reported to come from image identification errors (Johansson et al., 2020). We employed a multi-step process for image identification and tagging. Additionally, we conducted simulations to assess potential impact of unidentifiable images on the estimated density of snow leopards in our study (see section 2.6.2).

Image classification was done in two phases – image identification phase followed by the review phase. In the first phase, one or two researchers catalogued all the photos of snow leopards from each site. Rosette patterns from the face, limbs, rump, shoulder, upper parts of the tail and cheeks of the snow leopard were used to identify different individuals. In the second phase, two independent researchers reviewed all the individuals and especially those individuals that were

TABLE 2 Summary of the effort for double-observer surveys to estimate wild prey density of the snow leopard across 10 sites in Himachal Pradesh

Block	Year	Species	Effort (km)	Area (km^2)	Estimated abundance	Confidence interval	Density	Confidence	Detection probability (Observer 1)	Detection probability (Observer 2)	Mean group size	Estimated number of groups
Pin	2016	Ibex	45.5	298	224	224–256	0.75	0.75–0.86	0.93	0.77	14.00	16
Spiti	2017	Blue Sheep	96.5	816	810	790–850	0.99	0.97–1.04	0.89	0.86	20.26	40
		Ibex			94	82–127	0.12	0.10–0.15	0.84	0.63	11.71	8
		Combined			891	872–932	1.09	1.07–1.14	0.90	0.84	19.00	47
Tabo	2017	Blue Sheep	43.5	341	351	342–392	1.03	1.01–1.15	0.81	0.81	9.77	36
Hangrang	2017	Ibex	119.4	589	99	84–156	0.17	0.14–0.26	0.82	0.34	7.60	13
		Blue Sheep			454	435–505	0.77	0.74–0.86	0.85	0.68	9.90	46
		Combined			547	519–600	0.93	0.88–1.02	0.87	0.62	9.40	58
Bhaga	2018	Ibex	124	456	229	200–290	0.50	0.44–0.64	0.74	0.58	9.52	24
Miyar	2018	Ibex	88	604	164	142–254	0.27	0.23–0.42	0.65	0.65	10.92	15
Chandra	2018	Ibex	47.4	447	47	35–100	0.11	0.08–0.22	0.53	0.64	5.83	8
Baspa	2019	Blue Sheep	66.2	480	93	62–212	0.19	0.13–0.44	0.55	0.55	15.50	6
Kullu	2019	Blue Sheep	51.4	256	177	163–229	0.69	0.64–0.89	0.81	0.67	13.60	13
Bharmour	2019	Ibex	67.3	202	33	25–81	0.16	0.12–0.40	0.71	0.54	8.30	4

captured only once. In case of insufficient evidence towards identification as a new individual, we reverted the image as 'unidentified' or in case of a misidentification we re-assigned the identification. If both independent reviewers agreed on the changes, then they were retained. Disagreements between the reviewers were resolved by a third reviewer. All the changes proposed in the review stage were verified by a third reviewer who was also involved at the reviewing stage. All reviewers trained using the camtraining application (camtraining.globalsnowleopard.org). The third reviewer had an accuracy of 100% and confidence of 87% after training. Following the individual identification for each site, we conducted image comparisons across sites to check if any of the individuals were detected at more than one site. All snow leopard images were tagged using the digiKam image management software (https://www.digikam.org/) and tags were readout using the CamtrapR (Niedballa et al., 2016) package.

2.4 | Data analysis: Snow leopard density and population size

Snow leopard density and population size were estimated using multi-session SECR models. SECR models explicitly use the spatial information of detection location at the camera traps, accounting for the heterogeneity in captures due to animal activity centre location. Heterogeneity may arise because the probability of capture in a specific camera trap depends on its location relative to the animal's activity centre (Efford et al., 2009).

We conducted all analyses using the SECR 3.2.1 package in R (Efford, 2020). We used a multi-session SECR model in which sites corresponded to sessions as we expected densities to vary between sites. A habitat mask was specified (with buffer width of 28 km around the traps and spacing of 2 km between mask points, see SI 2 for details) to create the state space around the trap locations. The total area was defined by a single large polygon of potential snow leopard habitat of 26,112 km^2 in the state of Himachal Pradesh. This polygon represented the habitat of the snow leopard (regions above tree cover, typically at elevations higher than 3000 m but sometimes as low as 2000 m closer to river valleys). This polygon was prepared by extracting areas without tree cover from the Copernicus Global Land Cover Layers: CGLS-LC100 collection 2 (Buchhorn et al., 2015). At a given camera trap, the expected number of detections of an individual with activity centre at a distance d from the trap was assumed to have a half-normal shape defined by $\lambda^*\exp(-d^2/\sigma^2)$. Given the heterogeneity in density between sites, we modelled density as a parameter in the model, that is $D \sim$ site, $\lambda \sim 1$, $\sigma \sim 1$. We did not have enough detections for each site, hence σ (sigma) and λ (lambda) were modelled using information from all the sites. We tested the effect of pooling this information across sites on model estimates (see SI 2).

We calculated derived estimates of density and population size from the fitted model. We used derivednj() function in the secr package for estimating the sampling variance, which adapts the methods of Fewster et al. (2009) for SECR surveys, as detailed in the help files of the SECR package. Population size was estimated by multiplying

the stratum area (low occupancy, high occupancy and the unknown occupancy regions) with the density estimate for that stratum. We used derivednj() for estimating variance in the density estimates. In our model, information was pooled across sessions and independence between sessions could not be assumed. The derivednj() function uses the method of Buckland et al. (2001), as detailed in the help files of the SECR package, for calculating a weighted sum of variance. Abundance calculation was done for each stratum, and the estimates and the variance terms were summed to get a population size estimate for the entire area (see SI 2 for details of this method).

2.5 | Data analysis: Wild ungulate prey density and population size

The analysis was conducted using the 'BBRecapture' package following Suryawanshi et al. (2021) in R statistical and programming environment (R Core Team, 2020). Details on model fitting are available in SI 1.

We estimated wild ungulate density by dividing the estimated abundance by the total area sampled in each site. Total area sampled was obtained by adding up areas of all the surveyed blocks. Area of each block was obtained by demarcating it on a GIS platform (Google Earth Pro) post-survey by the team of surveyors.

2.6 | Sources of bias

We checked for two major sources of potential bias in snow leopard abundance estimation – inadequate sampling (Suryawanshi et al., 2019) and misidentification of individual snow leopards from camera trap photos (Johansson et al., 2020).

2.6.1 | Checking for sampling adequacy

We checked if dropping data from any one site significantly changed our density estimate or whether the new estimates (obtained after dropping data randomly from any one site) converged around the density estimate for the entire landscape. More details on methods and results can be found in SI 2.

2.6.2 | Assessing potential impact of unidentifiable images on the estimated density of snow leopards

In 187 of the 231 capture events, individual snow leopards were confidently identifiable, leaving 19% of the events unidentified (Table 1). These unidentified events, which were removed from the analysis, could have included additional captures of identified individuals as well as new individuals. To understand how unidentified events could gave affected density estimates, we simulated capture histories and estimated densities by dropping events from the 187 identified captures. We randomly dropped one to 60 (1%–32% of identified events) events sequentially from the data set and estimated the density each time. We repeated this 10 times each to estimate the variation in estimated density for each subset of the data. Events were randomly dropped from any of the 10 sites, ensuring that at least one individual was retained in each site. This gave us a total of 600 models with varying number of events and varying number of total individuals identified. We regressed the density estimates on the linear sum of the identified events and individuals to understand how dropping events and unidentified individuals might affect the density estimate.

3 | RESULTS

3.1 | Snow leopard population density and size

Our final image identification yielded 44 individual adult snow leopards from 187 detections across the 10 sites that were sampled. The sites varied in number of detections – Spiti from the high-occupancy stratum had 61 detections with nine individuals, Chandra from the low-occupancy stratum had 18 detections of three individuals and Kullu from the unknown stratum had 22 detections with two individual snow leopards.

Snow leopard density varied across sampling sites with a sevenfold difference between the highest and lowest density sites (Table 1). Tabo, Hangrang and Spiti had the highest densities of 0.37 (95% confidence interval [CI]: 0.18–0.72), 0.36 (95% CI: 0.18–0.73) and 0.30 (95% CI: 0.15–0.59) snow leopards per 100 km^2, whereas Bhaga from the low-density stratum recorded the lowest density of 0.05 (95% CI: 0.01–0.24) snow leopards per 100 km^2 (Table 1). The density estimates from the unknown stratum were generally low – Bharmour recorded a density of 0.06 (95% CI: 0.01–0.31) and Kullu recorded a density of 0.10 (95% CI: 0.03–0.35) snow leopards per 100 km^2. Overall, the snow leopard densities estimated for each stratum corresponded to the occupancy surveys – high-occupancy stratum showed a relatively high density of 0.30 (95% CI: 0.21–0.42) snow leopards per 100 km^2, low-occupancy stratum had a low density of 0.08 (95% CI: 0.05–0.12) and the previously unsampled stratum had a density of 0.08 (95% CI: 0.08–0.14) snow leopards per 100 km^2.

For our entire study region comprising all snow leopard habitat in the state of Himachal Pradesh, the estimated snow leopard density was 0.19 (95% CI: 0.12–0.31) per 100 km^2 and abundance was 51 (95% CI: 34–73) adult snow leopards. Detection probability at the activity centres λ (lambda) was estimated to be 0.018 (95% CI: 0.013–0.025). Sigma δ from our study was estimated to be 8.50 km (95% CI: 6.9–10.41 km).

3.2 | Wild ungulate population density

Blue sheep were recorded in four sites (Spiti, Tabo, Hangrang and Baspa), whereas Ibex were recorded in seven sites (all except Kullu, Tabo and Baspa). In general, areas with blue sheep (with the exception of Baspa) had higher ungulate densities than areas with Ibex. The

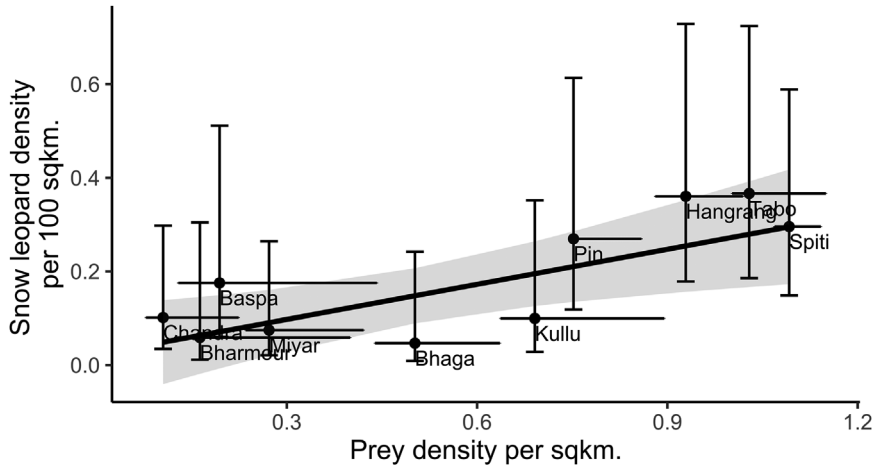

FIGURE 3 Snow leopard and wild ungulate density showed a positive correlation across the 10 sampled sites. Line represents predicted relationship from a weighted linear regression model (slope = 0.25, $SE = 0.08$, $P = 0.01$, $R^2 = 0.51$) and the shaded region represents 95% CI on the model prediction

highest wild ungulate density was recorded in Spiti (density: 1.09 individuals km^{-2}; 95% CI: 1.07–1.14 km^{-2}) and the lowest in Chandra (0.11 km^{-2}; 0.08–0.22 km^{-2}).

3.3 | Relationship between snow leopard and wild ungulate density

Snow leopard density showed a positive linear relationship with prey density (slope = 0.25, $SE = 0.08$, $P = 0.01$, $R^2 = 0.51$) (Figure 3). Sites with a high density of wild ungulates, such as Tabo (mean = 1.03, 95% CI: 1.01–1.15 prey km^{-2}) and Spiti (mean = 1.09, 95% CI: 1.07–1.14 prey km^{-2}), also had high densities of snow leopards (Tabo: 0.37 with 95% CI: 0.18–0.72; Spiti: 0.3 with 95% CI: 0.15–0.59 snow leopards per 100 km^2). On the other hand, Bharmour and Chandra that reported low densities of wild ungulates had low snow leopard densities (Figure 3).

3.4 | Errors in identification addressed during phase two (review) of image tagging

There were 231 events of snow leopard captures in camera traps across the 10 sites. At the review stage, 78.8% of the events had no conflict with the first tagging phase. Of the capture events, 63.6% could be identified and 15.2% were unidentifiable events. Within the 21.2% of events with conflicts at the review stage, 3.4% of the events were dropped during review, 10.0% were included and 7.8% were deemed misidentified. Within the misidentified events, 5.2% of the events were 'splits' leading to nine 'ghost' individuals, that is a misidentification error that leads to a split from an existing individual, and 2.6% shift errors, that is misidentification error that does not lead to any 'ghost' individuals but affect detection history. There were no combine errors.

In the first phase of tagging exercise, 52 unique individuals were identified, which after review were reduced to 44 individuals. Three new individuals were included after review, all of which were 'included' from unidentified images as opposed to being an outcome of fixing combine errors. Two single event capture individuals were dropped and categorized as unidentified. The remaining nine individuals that were dropped were 'ghost' individuals. The first phase of tagging had 18 single capture events, whereas the review stage had 10 single-capture events. The 'ghosts' included seven individuals that were captured on a single event, one individual that was captured twice (of which one event was dropped as unidentified) and one individual that was captured three times. The final capture history had a total of 187 identifiable events with 44 unique individuals.

3.5 | Simulations to assess potential impact of unidentifiable images on the estimated density of snow leopards

Out of the 600 simulated models, the total number of identified individuals in the capture history ranged from 38 to 44 (Figure 4). Linearly regressing the density estimate on the sum of the number of events and unique individuals identified showed a significant relationship ($F_{(2,598)} = 74.26$, $P < 0.001$, $R^2 = 0.20$). Estimated density increased marginally at the rate of 0.0008 snow leopards per 100 km^2 for every event that was dropped from the analysis ($t = -12.14$, $P < 0.001$).

4 | DISCUSSION

Our study represents among the first efforts towards assessing snow leopard populations at large regional scales using the two-step sampling approach proposed under the PAWS program (Sharma et al., 2019), which represents a coordinated global effort to estimate snow leopard abundance. We show that a stratified sampling design can address the potential spatial sampling biases that are common in snow leopard population studies (Johansson et al., 2020; Suryawanshi et al., 2019). Our estimated abundance of 51 (95% CI: 34–73) adult snow leopards for the state of Himachal Pradesh was 44% lower than the previously suggested figure of 90 snow leopards based on opinion and extrapolation (Bhatnagar et al., 2016). In fact, even the higher confidence interval of our abundance estimate (73 individuals) was almost 19% lower than the opinion-based estimate. In our study, it is also significant to note that the estimate of 51 snow leopards came from a

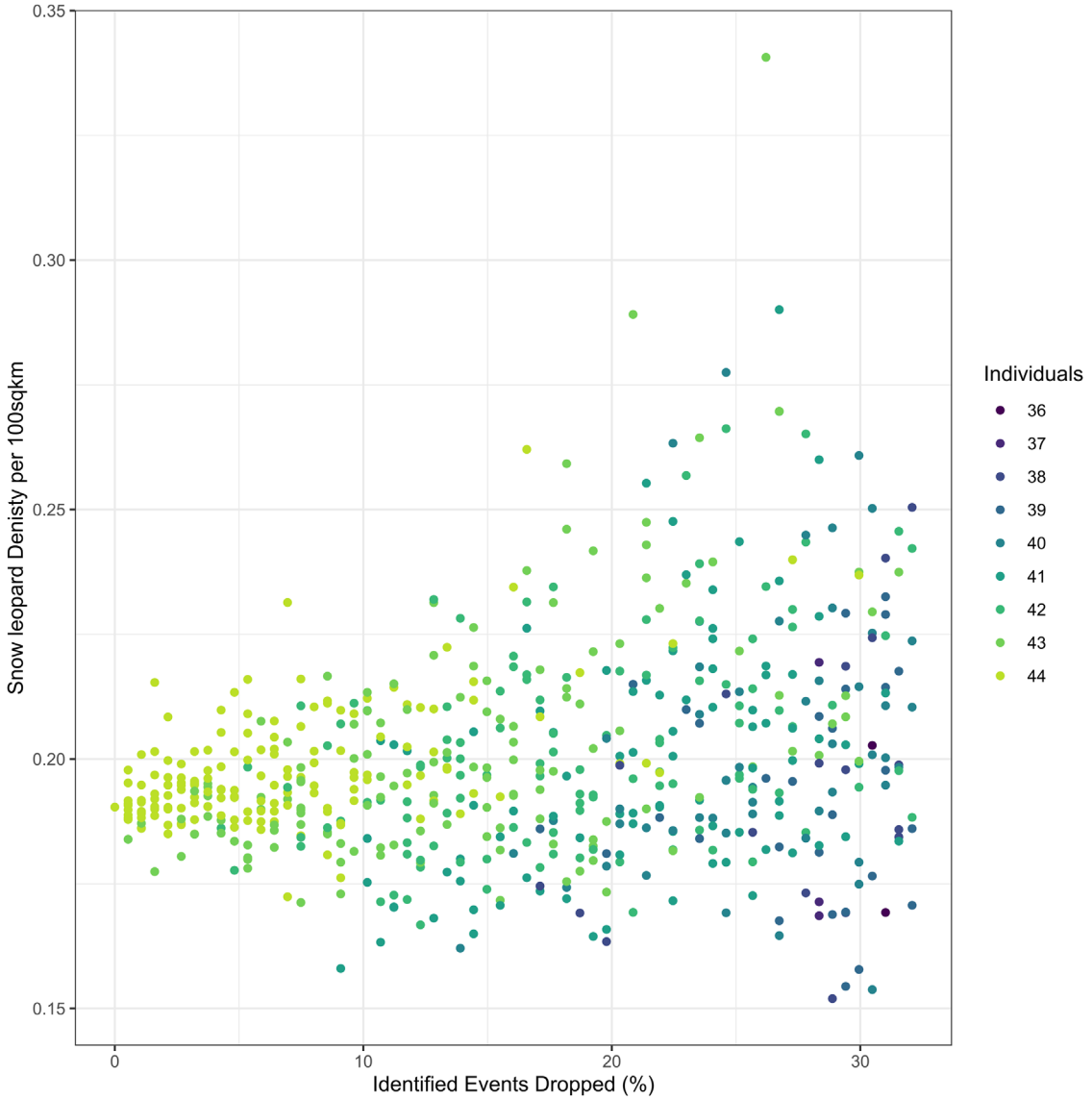

FIGURE 4 Estimated density of snow leopards when capture events were dropped randomly from the analysis. The colour of the dot indicates the number of individuals available for the analysis. The estimated density of snow leopards increased marginally (slope = 0.0008) with dropping of events

data set of 44 identified snow leopards, suggesting a rather low possibility of overestimation. Our study reiterates the possibility of significant overestimation of abundance in past population figures of snow leopards due to identification errors, sampling biases, sampling in small study areas or extrapolation (Johansson et al., 2020; Suryawanshi et al., 2019). Two past studies on snow leopards that involved sampling at least 1000 km^2 of area reported relatively low density estimates of 0.46 snow leopards per 100 km^2 at a site in Tajikistan (Kachel et al., 2017) and 0.83 snow leopards per 100 km^2 at a site in Mongolia (Sharma et al. 2014) compared to studies conducted over smaller areas (see Suryawanshi et al., 2019). Jackson et al. (2006) also noted that snow leopard density estimates reduced considerably when they sampled larger areas at their study site in Ladakh, India. A recent study estimated 144 snow leopards over an area of 14,174 km^2 based on molecular genetics data that actually discerned only 34 unique individuals within an area of 4393 km^2 in Nepal (Chetri et al., 2019). Such a high population estimate despite a low number of unique individuals is likely to have resulted from the use of a relatively large buffer area (twice the size of sampled area) for deriving the population size. We suggest exercising caution when using large buffer areas and recommend greater sampling effort in large landscapes using a stratified design.

We investigated whether any individual site from the 10 sampled sites may have had a disproportionate effect on the estimated density. Our results indicated that no single site influenced the estimated density significantly. However, we found that one site, Spiti (our largest site), did have a disproportionate impact on variance estimation of the sigma parameter. This was expected because estimation of sigma requires multiple captures of different snow leopards at different grids.

This is likely in sites that have high density of snow leopards and are large enough to have high abundance as well.

We used a two-phase camera trap image identification process to address the issue of overestimation because of human errors in identifying individual snow leopards from camera trap images. Our review phase confirmed a similar rate of image misidentification for some of the types of errors as were reported by Johansson et al. (2020). It is important to note that in our data set, 44 of the 231 (19%) snow leopard capture events remained unidentified after the review stage. Our simulations, where we randomly dropped snow leopard capture events to estimate the impact of unidentifiable images, showed that the effect size of dropping capture events on the density estimate was negligible. Theoretically, dropping unidentified images should not lead to a bias in the estimates. Lambda is typically used to model the expected encounter rate of every detection of an individual. In this case, it models the expected encounter rate of every identifiable detection of an individual, with the assumption that detections are unidentifiable at random as in the case of the simulations and not systematically biased towards detections from a particular trap or individual. Therefore, although the estimated density in our study did not change due to 19% of the capture events remaining unidentified and unused, the variation around the estimate may have increased as a result. From our data set, it appears that a conservative approach while identifying individual snow leopards from camera trap images may not affect the accuracy of the estimate but might affect the precision (Figure 4).

Abundance of large ungulate prey is a critical determinant of carnivore population density (Carbone & Gittleman, 2002; Suryawanshi et al., 2017) but estimates of prey densities are seldom used to assess the state of carnivore conservation. The relationship between the density of snow leopards and their prey in our study was linear, as expected from previous work (Suryawanshi et al., 2017). The slope of this relationship, however, was much lower in our study 0.25 ($SE = 0.08$) compared to 1.01 ($SE = 0.27$) in Suryawanshi et al. (2017). Our estimate of slope was closer to the estimate of slope of 0.5 (after accounting for variation) reported for tigers and their prey (Karanth et al., 2004). This is possibly due to the differences in density estimation methods used by Suryawanshi et al. (2017) who did not estimate a buffer area around the traps, and their study area sizes were relatively smaller (Suryawanshi et al., 2019). The positive correlation between snow leopard and wild ungulate density underscores the need to conserve the ungulate prey population which may be under threat from high-intensity grazing by migratory livestock, depredation by free-ranging dogs, illegal hunting and illegal wildlife trade (Ghoshal et al., 2019). Given the higher densities of both snow leopards and their prey in Tabo, Hangrang, Spiti and Pin, we recommend continued monitoring and conservation efforts at these sites. Additionally, efforts need to be undertaken to identify and mitigate the local factors that limit wild prey and snow leopard populations in low-density areas.

We used a stratified random sampling design based on an occupancy survey for our camera trap-based abundance estimation, and estimated snow leopard density for an area that was 1.5 times larger than the cumulative size of the study areas of all the previously published studies put together (Chetri et al., 2019; Khanal et al., 2020; Suryawanshi et al., 2019). Johansson et al. (2016) showed that 40% of the protected areas in the global range of the snow leopard are not large enough to cover the home range of a single adult male snow leopard. In our study, we detected snow leopards both inside and outside protected areas that formed part of our camera trapping area, confirming the need to sample beyond protected areas (Suryawanshi et al., 2019). Our study reiterates that density estimates obtained from small study areas, when extrapolated to much larger scales, such as regional, national or global snow leopard population estimates are likely to be unreliable.

The density estimates obtained for each of the 10 sites were qualitatively consistent with the stratification based on the occupancy data with low-occupancy sites emerging as low-density sites, and vice versa. Given our simulation exercise results that suggested that the overall density estimate was not sensitive to any particular site, our estimate can be considered representative of the entire snow leopard habitat in Himachal Pradesh. Our results support the value of using the two-step approach (using occupancy to inform camera trap-based sampling for abundance and density) as suggested by the technical committee of the PAWS Program (Sharma et al., 2019). This is the first study to validate the effectiveness of the PAWS-recommended study design.

The snow leopard was down-listed in the IUCN Red List of Threatened Species from Endangered to Vulnerable in 2017 (McCarthy et al., 2017). This change has been celebrated by some (Mallon & Jackson, 2017), whereas on the other hand, this decision has been challenged by many scientists, institutions and country governments, citing the use of poor-quality information on the global population of snow leopards (Ale & Mishra, 2018; Johansson et al., 2020; Suryawanshi et al., 2019). For the Red List assessment that led to down-listing of snow leopards, 63 of the 69 study samples used were based on opinions and sign surveys (see Ale & Mishra, 2018). Our results reiterate the flaws involved in snow leopard population estimates based on opinions and inappropriate study designs, and using them for species status assessments.

Assessing the conservation status of rare and elusive species of global conservation concern is challenging but we discourage the use of opinion-based expert surveys to arrive at population numbers. We recommend using robust study design alongside technological advancements in camera trapping, and in molecular genetics and statistical tools for national- and international-level prioritization of species and landscapes for conservation.

ACKNOWLEDGEMENTS

This project was supported by the Himachal Pradesh Forest Department. This would not have been possible without the help and support of various Forest Department officials at the state level and across each site. A special thanks to the field staff of Nature Conservation Foundation and various guides, porters and volunteers across each site, whose tireless efforts were invaluable in procuring the data needed for this paper. Additionally, we would like to extend our acknowledgement to the Police Departments, as they were extremely proactive in inquiring about any missing cameras and the Indo-Tibetan Border Police who gave us permission to survey areas under their jurisdiction. Lastly, we would like to thank all the communities we visited during the

field work. We were always welcomed with open arms and it was their invaluable knowledge and advice that led us to navigate the field surveys. We thank the British Ecological Society, Disney Conservation Fund, the National Geographic Society for partial funding. We thank the Cholamandalam Investment and Finance Company Limited for supporting training workshops for camera trapping work.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

The idea was conceived by KS, AB and CM. The study was designed by KS, AB, AG and CM. Data were collected by DR, AK, MK, JP, AM and AR. Data were analysed by MS, AR, KS, HK, MK, AM and DR. The first draft of the manuscript was written by KS, MS, AR and MK. All authors contributed to writing the manuscript.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1002/2688-8319.12115.

DATA AVAILABILITY STATEMENT

The data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0cfxpnw3p (Sharma, 2021). Exact GPS locations have been encrypted. Please see usage notes in Dryad for more details and contact the authors if you need to access this encrypted information.

ORCID

Manvi Sharma https://orcid.org/0000-0002-8236-6342

REFERENCES

Akcakaya, H. R., Ferson, S., Burgman, M. A., Keith, D. A., Mace, G. M., & Todd, C. (2000). Making consistent IUCN classifications under uncertainty. *Conservation Biology*, *14*, 1001–1013. https://doi.org/10.1046/j.1523-1739.2000.99125.x

Ale, S. B., & Mishra, C. (2018). The snow leopard's questionable comeback. *Science*, *359*, 1110. https://doi.org/10.1126/science.aas9893

Alexander, J. S., Gopalaswamy, A., Shi, K., & Riordan, P. (2015). Face value: Towards robust estimates of snow leopard densities. *PLoS ONE*, *10*, e0134815. https://doi.org/10.1371/journal.pone.0134815

Bagchi, S., & C. Mishra. (2006). Living with large carnivores: Predation on livestock by the snow leopard (*Uncia uncia*). *Journal of Zoology*, *268*(3), 217–24. https://doi.org/10.1111/j.1469-7998.2005.00030.x. https://doi.org/10.1111/j.1469-7998.2005.00030.x

Bhatnagar, Y. V., Mathur, V. B., Sathyakumar, S., Ghoshal, A., Sharma, R. K., Bijoor, A., Raghunath, R., Timbadia, R., & Lal, P. (2016). South Asia: India. In T. McCarthy & D. Mallon (Eds.), *Snow leopards: Biodiversity of the world: Conservation from genes to landscapes* (pp. 457–569). Elsevier.

Borchers, D. L., & M. G. Efford. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, *64*, 377–385 https://doi.org/10.1111/j.1541-0420.2007.00927.x

Buchhorn, M., Smets, B., Bertels, L., Lesiv, M., Tsendbazar, N. - E., Herold, M., & Fritz, S. (2015). *Copernicus Global Land Service: Land Cover 100m: Epoch 2015: Globe*. Dataset of the global component of the Copernicus Land Monitoring Service 2019.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling: Estimating abundance of biological populations*. Oxford University Press.

Caro, T. (2010). *Conservation by proxy: Indicator, umbrella, keystone, flagship, and other surrogate species*. Island Press.

Carbone, C., & Gittleman, J. L. (2002). A common rule for the scaling of carnivore density. *Science*, *295*, 2273–2276. https://doi.org/10.1126/science.1067994

Chetri, M., Odden, K. Sharma, Ø. Flagstad, & P. Wegge. (2019). Estimating snow leopard density using fecal DNA in a large landscape in north-central Nepal. *Global Ecology and Conservation*, *17*, e00548. https://doi.org/10.1016/j.gecco.2019.e00548

Efford, M. G., Borchers, D. L., & Byrom, A. E. (2009). Density estimation by spatially explicit capture–recapture: Likelihood-based methods. In D. L. Thomson, E. G. Cooch, & M. J. Conroy (Eds.), *Modeling demographic processes in marked populations* (pp. 255–269). Springer.

Efford, M. G. (2020). *secr: Spatially explicit capture-recapture models*. R package version 4.2.2. https://CRAN.R-project.org/package=secr

Fewster, R. M., Buckland, S. T., Burnham, K. P., Borchers, D. L., Jupp, P. E., Laake, J. L., & Thomas, L. (2009). Estimating the encounter rate variance in distance sampling. *Biometrics*, *65*, 225–236.

Forsyth, D. M., & Hickling, G. J. (1997). An improved technique for indexing abundance of Himalayan thar. *New Zealand Journal of Ecology*, *21*(1), 97–101.

Ghoshal, A., Bhatnagar, Y., Pandav, B., Sharma, K., Mishra, C., Raghunath, R., & Suryawanshi, K. (2019). Assessing changes in distribution of the Endangered snow leopard *Panthera uncia* and its wild prey over 2 decades in the Indian Himalaya through interview-based occupancy surveys. *Oryx*, *53*(4), 620–632.

GSLEP Secretariat. (2017). *The Bishkek Declaration 2017*. http://www.globalsnowleopard.org/blog/2017/08/28/the-bishkek-declaration-2017-caring-for-snow-leopards-and-mountains-our-ecological-future/

Immerzeel, W. W., Van Beek, L. P., & Bierkens, M. F. (2010). Climate change will affect the Asian water towers. *Science*, *328*(5984), 1382–1385. https://doi.org/10.1126/science.1183188

Jackson, R. M. (1996). *Home range, movements and habitat use of snow leopard (Uncia uncia) in Nepal (PhD thesis)*. University of London.

Jackson, R. M., Roe, J. M., Wangchuk, R., & Hunter, D. O. (2006). Estimating snow leopard population abundance using photography and capture-recapture techniques. *Wildlife Society Bulletin*, *34*, 772–781. https://doi.org/10.2193/0091-7648(2006)34%5b772:ESLPAU%5d2.0.CO;2

Janečka, J. E., Jackson, R., Yuquang, Z., Diqiang, L., & Munkhtsog, B. (2008). Population monitoring of snow leopards using noninvasive collection of scat samples: A pilot study. *Animal Conservation*, *11*, 401–411. https://doi.org/10.1111/j.1469-1795.2008.00195.x

Jhala, Y. V., Qureshi, Q., & Nayak, A. K. (Eds.). (2019). *Status of tigers, co-predators and prey in India 2018*. Summary report. TR No./2019/05. National Tiger Conservation Authority, Government of India, New Delhi & Wildlife Institute of India, Dehradun.

Johansson, Ö., Rauset, G. R., Samelius, G., McCarthy, T., Andrén, H., Tumursukh, L., & Mishra, C. (2016). Land sharing is essential for snow leopard conservation. *Biological Conservation*, *203*, 1–7. https://doi.org/10.1016/j.biocon.2016.08.034

Johansson, Ö., Samelius, G., Wikberg, E., Chapron, G., Mishra, C., & Low, M. (2020). Identification errors in camera trap studies result in systematic population overestimation. *Scientific Reports*, *10*, 6393. https://doi.org/10.1038/s41598-020-63367-z

Kachel, S. M., McCarthy, K. P., McCarthy, T. M., & Oshurmamadov, N. (2017). Investigating the potential impact of trophy hunting of wild ungulates on snow leopard Panthera uncia conservation in Tajikistan. *Oryx*, *51*, 597–604. https://doi.org/10.1017/S0030605316000193

Karanth, K. U. (1995). Estimating tiger *Panthera tigris* populations from camera trap data using capture–recapture models. *Biological Conservation*, *71*, 333–338. https://doi.org/10.1016/0006-3207(94)00057-W

Karanth, U., Nichols, J., Kumar, N., Link, W., & Hines, J. (2004). Tigers and their prey: Predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Science*, *101*, 4854–4858. https://doi.org/10.1073/pnas.0306210101

Khanal, G., Mishra, C., & Suryawanshi, K. R. (2020). Relative influence of wild prey and livestock abundance on carnivore-caused livestock predation. *Ecology and Evolution*, *10*, 11787–11797. https://doi.org/10.1002/ece3.6815

Li, J., B. V. Weckworth, T. M. McCarthy, X. Liang, Y. Liu, R. Xing, D. Li, et al. (2020). Defining priorities for global snow leopard conservation landscapes. *Biological Conservation*, *241*(January), 108387. https://doi.org/10.1016/j.biocon.2019.108387

Mallon, D. P., & Jackson, R. M. (2017). A downlist is not a demotion: Red list status and reality. *Oryx*, *51*, 605–609. https://doi.org/10.1017/S0030605317000606

McCarthy, T., Mallon, D., Sanderson, E. W., Zahler, P., & Fisher, K. (2016). What is a snow leopard? Biogeography and status overview. In T. McCarthy & D. Mallon (Eds.), *Snow leopards* (pp. 23–42). Elsevier.

McCarthy, T., Mallon, D., Jackson, R., Zahler, P., & McCarthy, K. (2017). *Panthera uncia*. The IUCN Red List of Threatened Species 2017.

MoEFCC. (2019). *Snow leopard population assessment in India: Population assessment of world's snow leopards*. Ministry of Environment, Forest and Wildlife; Wildlife Institute of India; Nature Conservation Foundation-Snow Leopard Trust; and Global Snow Leopard and Ecosystem Protection Program-PAWS Advisory Panel.

Mondal, S., Karanth, U., Kumar, N., Gopalaswamy, A., Andheria, A., & Ramakrishnan, U. (2009). Evaluation of non-invasive genetic sampling methods for estimating tiger population size. *Biological Conservation*, *142*, 2350–2360. https://doi.org/10.1016/j.biocon.2009.05.014

Niedballa, J., Sollmann, R., Courtiol, A., & Wilting, A. (2016). camtrapR: An R package for efficient camera trap data management. *Methods in Ecology and Evolution*, *7*(12), 1457–1462. https://doi.org/10.1111/2041-210X.12600

R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Sharma, M. (2021). Raw datafiles for SECR analyses. *Dryad Dataset*. https://doi.org/10.5061/dryad.0cfxpnw3p

Sharma, K., Bayrakcismith, R., Tumursukh, L., Johansson, O., Sevger, P., McCarthy, T., & Mishra, C. (2014). Vigorous dynamics underlie a stable population of the endangered snow leopard *Panthera uncia* in Tost Mountains, south Gobi, Mongolia. *Plos One*, *9*, e101319. https://doi.org/10.1371/journal.pone.0101319

Sharma, K., Borchers, D., Mackenzie, D., Durbach, I., Sutherland, C., Nichols, J. D., Lovari, S., Zhi, L., Khan, A. A., Modaqiq, W., McCarthy, T. M., Alexander, J. S., & Mishra, C. (2019). *Guidelines for estimating snow leopard abundance and distribution using a combination of spatial capture-recapture and occupancy models*. Submitted to the Steering Committee of the Global Snow Leopard and Ecosystem Protection Program; with financial support from Global Environment Facility, United Nations Development Program and Snow Leopard Trust.

Sollmann, R., Gardner, B., & Belant, J. L. (2012). How does spatial study design influence density estimates from spatial capture-recapture models? *Plos One*, *7*(4), e34575. https://doi.org/10.1371/journal.pone.0034575

Snow Leopard Network (2014). *Snow leopard survival strategy*. Author.

Suryawanshi, K. R., Bhatnagar, Y. V., & Mishra, C. (2012). Standardizing the double-observer survey method for estimating mountain ungulate prey of the endangered snow leopard. *Oecologia*, *169*(3), 581–590. https://doi.org/10.1007/s00442-011-2237-0

Suryawanshi, K. R., Redpath, S. M., Bhatnagar, Y. V., Ramakrishnan, U., Chaturvedi, V., Smout, S. C., & Mishra, C. (2017). Impact of wild prey availability on livestock predation by snow leopards. *Royal Society Open Science*, *4*, 170026. https://doi.org/10.1098/rsos.170026

Suryawanshi, K. R., Khanyari, M., Sharma, K., Lkhagvajav, P., & Mishra, C. (2019). Sampling bias in snow leopard population estimation studies. *Population Ecology*, *61*(3), 268–276. https://doi.org/10.1002/1438-390X.1027

Suryawanshi, K. R., Mudappa, D., Khanyari, M., Shankar, T. R. S., Rathore, D., Ananda Kumar, M., & Patel, J. (2021). Population assessment of the Endangered Nilgiri tahr Nilgiri tragus hylocrius in the Anamalai Tiger Reserve, using the double-observer survey method. *Oryx*, *55*(1), 66–72.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Suryawanshi, K., Reddy, A., Sharma, M., Khanyari, M., Bijoor, A., Rathore, D., Jaggi, H., Khara, A., Malgaonkar, A., Ghoshal, A., Patel, J., & Mishra, C. (2021). Estimating snow leopard and prey populations at large spatial scales. *Ecological Solutions and Evidence*, *2*, e12115. https://doi.org/10.1002/2688-8319.12115