Camera traps placed to detect predators underestimate prey densities

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Abstract Mountain ungulates play an important role in ecosystems as primary consumers and as prey for rare predators. Monitoring their populations is therefore critical for conservation efforts. Within the 12 countries comprising the range of the snow leopard *Panthera uncia*, camera traps are routinely deployed to estimate numbers of this apex predator, providing an opportunity to also estimate numbers of their prey using bycatch data. However, the relative accuracy of the resulting prey density estimates compared to field surveys targeted specifically at prey species was unknown. We compared the performance of distance sampling based on camera-trap data with field surveys to estimate population densities of bharal Pseudois nayaur. We assessed estimates of bharal numbers from cameras placed to detect snow leopards (where ungulate captures presented bycatch data) against estimates from cameras placed specifically to detect bharal and then compared both with an independent estimate of bharal density from double-observer surveys and a total count of all bharal in the study area. The double-observer field surveys suggested a density of 1.94 bharal/km², which was similar to the density derived from the total count (1.92 bharal/km²). By comparison, we estimated density to be 2.11 bharal/km² from camera-based distance sampling and 0.35 bharal/km² from cameras placed to detect snow leopards (bycatch data). The density estimate from the ungulate bycatch data was significantly lower than that from the double-observer field survey and from the total count. It was also less precise, more costly and more time-consuming to obtain. Our results caution against using bycatch data from surveys designed for predators to estimate ungulate prey densities and indicate that tailored survey methods are required.

Keywords Bycatch data, camera trap, distance sampling, double-observer, mountains, population density, total count, ungulates

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Introduction

The accurate and statistically robust estimation of wildlife population densities is a challenge for management and conservation (Nichols & Williams, 2006). Methods need to deliver accurate estimates, whilst also being feasible both financially and technically. Robust population estimates repeated at intervals can help to determine population trends (Mihoub et al., 2017), and a baseline population size is invaluable when framing conservation objectives and setting priorities (Bull et al., 2014).

The number of wild ungulate prey in an area is a key determinant of carnivore population size (Karanth et al., 2004; Suryawanshi et al., 2021) and directly affects ecosystem health through nutrient cycling and grazing pressure (Bagchi & Ritchie, 2010). Whilst various methods exist to estimate ungulate densities, it remains a particular challenge in remote mountainous areas (Singh & Milner-Gulland, 2011) where there is also a comparative lack of research capacity (Mishra et al., 2017), such as in Central and South Asia.

Double-observer surveys use the robust mark-recapture framework to estimate population size and have been used extensively to estimate mountain ungulate populations (Suryawanshi et al., 2012, 2021; Khanyari et al., 2021; Khara et al., 2021; Moheb et al., 2023). However, these surveys require trained observers and considerable field effort. Alternatively, unmarked animal populations can be estimated using distance sampling with camera traps (Howe et al., 2017; Palencia et al., 2021). For example, Pal et al. (2021) used an extension of the distance sampling method to accommodate camera-trap data for estimating numbers of group-living bharal Pseudois nayaur (also known as blue sheep) and solitary Himalayan musk deer Moschus leucogaster. Harris et al. (2020) tested camera-based distance sampling within a captive population of bighorn sheep Ovis canadensis and found that true abundance was always within their estimated 90% confidence bounds, suggesting this method is suitable for surveying Caprinae.

Ungulates are often monitored using data obtained as a byproduct of surveys targeting predators, which are frequently charismatic and attract attention as umbrella and flagship species (Sergio et al., 2008). The snow leopard

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Panthera uncia is a flagship species across High Asia where its key prey species are bharal, argali Ovis ammon and Asiatic ibex Capra sibirica. In 2017, the 12 countries within the snow leopard range (Afghanistan, Bhutan, China, India, Kazakhstan, Kyrgyzstan, Mongolia, Nepal, Pakistan, Russia, Tajikistan and Uzbekistan) initiated a collaborative effort called PAWS (Population Assessment of the World's Snow Leopards) to estimate national and global populations of snow leopards in the wild (GSLEP Secretariat, 2017). Camera traps and faecal DNA sampling were used to collect data on snow leopards, with the additional possibility of estimating ungulate densities from camera-trap bycatch data. However, the accuracy of ungulate population estimates from camera traps placed to detect snow leopards was untested at the time.

Our objective in this study was to compare the performance of camera-based distance sampling to estimate the population density of a wild mountain ungulate, the bharal, with estimates obtained from field surveys using the double-observer method and a total count. We also compared two camera-based distance sampling strategies: firstly from cameras placed to detect snow leopards (generating ungulate bycatch data) and secondly from cameras placed to maximize detection of ungulates. We then compared these two population estimates to double-observer estimates and a total count (the latter provided the minimum number of bharal in the area, for reference).

Theoretically, camera traps placed according to a study design for distance sampling should yield population density estimates comparable to robustly conducted field surveys. The theoretical framework for distance sampling is well described, with software and advice readily available both for designing studies and analysing data (Buckland et al., 2001, 2004, 2015; Howe et al., 2017). We expected double-observer surveys to be relatively accurate given their extensive use in the study area. This method is based on two observers independently and concurrently counting animals in a defined area (Suryawanshi et al., 2012; Sharma et al., 2024). By comparison, we expected data taken from camera traps placed in microhabitats suited to snow leopards to underestimate bharal density because the assumptions of camera-based distance sampling could be violated by compromised identification of animals only partially visible in the camera-trap images, and animals directly in front of the cameras being missed because of trigger delays (Howe et al., 2017). In the absence of a reliable estimate of ungulate population density in the study area, we used the total count as our benchmark and any densities below that were interpreted as underestimates (Fig. 1).

Study area

The Upper Spiti Landscape (Fig. 2) in the Indian Trans-Himalaya is a high-altitude (3,500–6,700 m) region. The

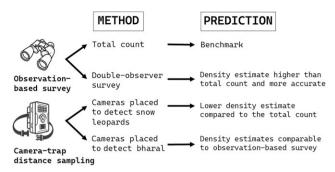


Fig. 1 Schematic representation of our study design and predictions.

temperature ranges from -35 °C to 30 °C and precipitation is largely in the form of winter snowfall. The vegetation is broadly classified as dry alpine steppe (Champion & Seth, 1968). Large mammals in the region include the bharal, Asiatic ibex and their predators, the snow leopard and grey wolf *Canis lupus*. Spiti supports c. 10,600 people spread across 30 villages. Most are agro-pastoralists, cultivating a single crop in summer and raising livestock in the surrounding pastures. Within this region, we have been monitoring snow leopards with camera traps and ungulates through double-observer surveys for 14 years.

Methods

Field survey

We conducted a double-observer survey to estimate bharal abundance (Forsyth & Hickling 1997; Suryawanshi et al., 2012) across the 411 km² study area (Fig. 2). This method uses mark-recapture framework, where the unit being marked and recaptured is an ungulate group rather than an individual animal, as is more common for individually identifiable species such as the snow leopard (Forsyth & Hickling, 1997). Groups, even if temporary, are identifiable by their size, age–sex composition, and location and were defined on the basis of distance from the observer and spatial extent of the group, time of observation and coordinated or cohesive behaviour such as moving or foraging together (Kasozi & Montgomery, 2020).

The Upper Spiti Landscape was divided into 15 smaller blocks informed by the area's topography and ease of conducting surveys (Fig. 2). The survey was conducted in the last week of May 2022 (immediately prior to the camera-trapping surveys), took 3 days to complete and involved eight observers who walked 99 km in total. The survey routes followed transects that were chosen based on accessibility and maximizing viewshed of each block; many of them were along ridge lines. On each survey route, two teams (with one or two observers per team) surveyed each block independently of each other, with the second team

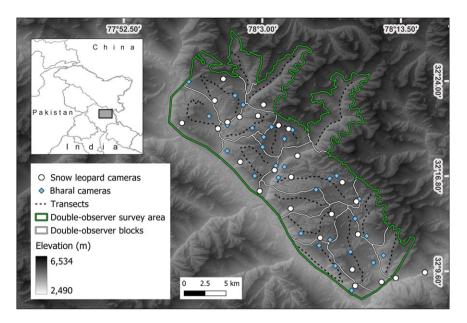


Fig. 2 Study area in the Upper Spiti Landscape in the Indian Trans-Himalaya where surveys of snow leopard *Panthera uncia* and bharal *Pseudois nayaur* were conducted. The positions of camera traps and the routes of survey transects within the sampling blocks are shown. Note that the transects for the double-observer population estimates were also used to generate total counts of bharal.

starting their survey c. 30 minutes after the first team. Over the 3 days, all blocks were covered, with different blocks being surveyed by different teams. Observers used 8×40 binoculars to search for and count individual ungulate groups and the number of animals in each group. We identified ungulate groups by their size, age-sex composition, geographical location and any other unique features such as individuals with broken horns. We aimed to start surveys at sunrise, to control for the effect of time of day on bharal activity and grouping patterns; surveys in three blocks were started later in the morning but no later than 10.00 (Fattorini et al., 2019). The observers involved in this study have conducted double-observer field surveys in the same area for many years and are trained to ensure robust application of the method. For further details of the doubleobserver method, see Suryawanshi et al. (2012, 2021).

Camera-trap surveys

We used Reconyx Hyperfire (Reconyx, USA) camera traps. They were set to work continuously in rapid-fire mode, taking five images at each trigger, with a trigger interval of <1 s. The cameras were in place for 60 days from 4 June–4 August 2022. Elevation was recorded while placing the camera traps; ruggedness, slope and aspect were derived using satellite data (see sampling bias section below).

Camera trapping for snow leopards generating ungulate bycatch data As part of an annual monitoring programme, we placed 25 camera traps in locations suitable for snow leopard monitoring in the Upper Spiti Landscape. We divided the study area into a 4×4 km grid to estimate snow

leopard densities (Alexander et al., 2015). We deployed at least one camera in each cell apart from those that were inaccessible or under permafrost. We chose camera locations based on the prevalence of snow leopard signs such as hair, scat, scrape or urine spray marks, and in suitable microhabitats to maximize detection. We reviewed all images from these cameras to identify bharal captures (i.e. bycatch data) that could be analysed using the camerabased distance sampling framework.

Dedicated camera trapping for ungulates We deployed 30 camera traps using a systematic design with a random origin. We generated a random point in each 4×4 km grid cell and placed a camera at that location or as close as possible if the point was inaccessible. We positioned all cameras to face the same compass orientation, 40-50 cm above the ground and angled to be parallel to the slope of the ground. We calibrated image measurements against actual measurements in the landscape by placing natural marks (e.g. rocks or shrubs) in the camera's field of view at 1 m intervals. These marks were used during image analysis to determine the position of the animal relative to the camera.

Analysis of double-observer surveys

We estimated the abundance of bharal in the Upper Spiti Landscape using the package *multimark* in *R 4.4.1* (McClintock, 2015; R Core Team, 2024) with a Bayesian framework. We analysed the number of groups as recommended by Suryawanshi et al. (2012) and based on the capture–recapture framework, where a group was coded '1–1' if recorded by both observer teams, '1–0' if recorded by the first team only, and '0–1' if recorded by the second team

only. We used the Mt model (i.e. capture probabilities vary with time; Otis, 1978) as we expected detection probability to vary across the two observer teams and surveys (Suryawanshi et al., 2012). To estimate the total number of groups of wild ungulates (\hat{G}) , we fit the Mt model using the *markClosed* function in R with uninformed uniform priors and carried out 10,000 Markov chain Monte Carlo iterations with a 1,000 burn-in. We interpreted the estimated detection probability for occasions 1 and 2 as the detection probability for observer teams 1 and 2.

We calculated bharal population abundance (N_{est}) as a product of the estimated number of groups (\hat{G}) and the estimated mean group size (μ), given by Equation 1:

$$N_{est} = \widehat{G} \times \mu \tag{1}$$

To estimate the 95% confidence intervals of the population using the variance in \hat{G} and $\mu,$ we generated a distribution of \hat{G} by bootstrapping it 10,000 times with replacement. We generated a distribution of N_{est} by multiplying 10,000 random draws of \hat{G} weighted by the posterior probability and draws of $\mu.$ The median of the resulting distribution was the estimated bharal abundance (N_{est}) and the 2.5 and 97.5 percentiles were used as the 95% confidence intervals (Supplementary Table 1, Supplementary Figs 2, 3, 4).

We calculated the total bharal count (abundance) as the sum of the individuals in unique groups detected by either of the two sets of observers. We identified unique groups from their size, age—sex composition, location in the landscape and any other distinct features. This avoided the risk of double-counting groups that were frequently sighted and ensured that abundance was a robust minimum count. We then calculated bharal density by dividing the total count abundance by the study area.

Camera-based distance sampling analysis

Distance sampling using camera traps requires that the distance between the animal and the camera in snapshot moments is known, to ensure that animal movement does not bias the distribution of detection distances (Howe et al., 2017). Observation distances between camera traps and animals were recorded at 2 s intervals. We used natural features in the cameras' field of view during the camera deployment to estimate the distance of the animal from the camera, based on our initial calibration.

We followed Howe et al. (2017) in our analysis of camera-based distance sampling data using Equation 2 to calculate *D*, the density:

$$D = \frac{Y}{\pi * w^2 * e * p} \tag{2}$$

Here $e = \theta * \frac{H}{2} * \pi * t$ is the sampling effort, t is the length of the time step between snapshot moments, which is a fixed value of 2 s, and θ is the angle of the field of view of the

camera trap. H is the total camera survey effort, w is the truncation distance and p is the estimated probability that an animal within distance w is detected by a camera trap. This is estimated from a detection function model fitted to animal distances from camera (Buckland et al., 2015). Y is the number of encounters, equal to the number of independent photographic sequences.

We left-truncated the data when fewer than expected detections near the camera traps were recorded (Howe et al., 2017), and right-truncated the data when the detection probability was lower than 0.1. To account for the limited field of view of the camera traps, we applied a spatial multiplier based on the camera's detection angle. Specifically, the cameras sampled a 42° sector of the full 360° circle around the camera trap, and this proportion (42/360), in radians, was used to adjust the effective area surveyed in the analysis (Howe et al., 2017). We specified an activity period between 06.00-18.00 as the sampling period based on the activity of bharal derived from the camera-trap data. We corrected for the bias caused by animals being unavailable for detection by calculating the mean proportion of animals that were active during the period selected for analysis and incorporating this proportion in the density estimates (Supplementary Tables 2-6, Supplementary Figs 5-9; Pal et al., 2021).

Testing for sampling bias

To test for sampling bias in our camera trapping design across the landscape, we compared elevation, ruggedness, slope and aspect of camera-trap locations and 100 randomly generated points, using a non-parametric Wilcoxon rank sum test for elevation, ruggedness and slope, and a Manly selectivity test for aspect (Manly et al., 2022). We resampled terrain data from the Shuttle Radar Topography Mission at 1 km resolution (Jarvis et al., 2008). Pictures taken more than 30 min apart were treated as independent capture events. We calculated the camera-level encounter rate for blue sheep by summing up the number of independent captures for each camera and dividing this by the total camera-trap effort (O'Brien et al., 2003). We tested camera-trap encounter rates for spatial autocorrelation by calculating Moran's I, where a value close to o suggests no spatial autocorrelation, a value of +1 suggests positive spatial autocorrelation and a value of -1 suggests spatial dispersion.

Statistical comparison of densities

We calculated z-scores to test for a statistical difference between density estimates from camera-based distance sampling and double-observer surveys. A z-score is a statistical measure that describes how many standard deviations a data point is from the mean of a distribution and is a way to standardize data and compare it within the context of a normal distribution (Zar, 1999; Forsyth & Hickling, 1997). We calculated z-scores using Equation 3:

$$Z = \frac{(Estimate_1 - Estimate_2)}{\sqrt{Standard\ Error_1^2 + Standard\ Error_2^2}}$$
(3)

Further details on the calculation of the z-score can be found in Supplementary Table 7.

Practical application

In addition to comparing these methods based on their z-scores and against the minimum count of bharal, we also evaluated their practical application. We included the process of acquiring, storing, processing and analysing data to generate density estimates of bharal. We assessed the overall budget, equipment, human resources and time required to carry out the surveys, and the post-survey processing time. We discuss the merits of double-observer surveys and camera-based distance sampling (combing bharal and snow leopard surveys for this analysis). We provide an assessment of cost and effort (hours) and identify some key considerations.

Results

Testing for sampling bias

The mean values of ruggedness and slope for the 55 cameratrap locations (25 snow leopard and 30 ungulate camera traps) were not significantly different from 100 random points (P > 0.05 in each case, Wilcoxon rank sum test; Supplementary Fig. 1) indicating that there was no bias. Similarly, there was no bias in the elevation of cameras placed for ungulates but there was a significant difference between snow leopard camera traps and randomly selected points (P = 0.027, Supplementary Fig. 1). The Manly selectivity test also indicated no particular aspect category was disproportionately sampled for either camera-trap design (Supplementary Fig. 1). Encounter rates were variable amongst camera-trap locations and did not show any spatial autocorrelation for the cameras placed for ungulates (Moran's I = -0.02) or snow leopards (Moran's I = -0.17).

Comparison of bharal density estimates from different methods

The double-observer survey yielded a density of 1.94 bharal/km² (95% CI 1.53–2.42 bharal/km²), with detection probability of observer 1 being 0.60 and observer 2 being 0.75. This is similar to the density estimate from the total count (1.92 bharal/km²; Supplementary Table 1, Supplementary Figs 2–4). In comparison, the density estimate from cameras placed to detect ungulates was 2.21 bharal/km² (95% CI 0.74–6.04 bharal/km²), whereas that from cameras placed to detect snow

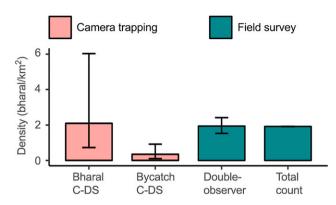


Fig. 3 Bharal density estimated by four methods: camera-based distance sampling (C-DS) using images from cameras placed specifically to detect ungulates, camera-based distance sampling using bycatch data from cameras placed to detect snow leopards, double-observer surveys along transect routes in 15 study blocks, and total bharal counts calculated from transect counts and the area of the study blocks.

leopards (with bharal bycatch data) was 0.35 bharal/km² (95% CI 0.13–0.92 bharal/km²). Therefore, bharal density estimates using camera-based distance sampling from bycatch data were statistically different from double-observer density estimates (z = 5.24, P < 0.05) and were also below the minimum count (Fig. 3). Density estimates from the two camera-based distance sampling designs were not significantly different (z = -1.29, P = 0.19). Density estimates from camera-based distance sampling of bharal were not significantly different from the double-observer survey estimates (z = -0.12, P = 0.90). The analysis is summarized in Supplementary Tables 2–6 and Supplementary Figs 5–10.

Practical application

We summarize information on logistics gathered before, during and after the surveys using double-observer and camera-based distance sampling in Table 1. The double-observer method was less resource-intensive compared to the camera-based distance sampling method. Specifically, the cost of time invested and money spent was higher for camera-based distance sampling because of the specialist equipment required as well as the lengthy post-processing time. However, if camera traps are already available and in place, the cost is reduced significantly.

Discussion

We compared the performance of camera-based distance sampling to estimate the population density of a wild mountain ungulate, the bharal, with estimates obtained from field surveys using the double-observer method and a reference minimum population size derived from a total count of all ungulate groups. In addition, we compared population estimates derived from camera traps placed to

TABLE 1 Summary of practical considerations for the double-observer and camera-based distance sampling methods of estimating ungulate density in a mountainous region.

detect snow leopards but yielding ungulate bycatch data with those from cameras placed specifically to detect ungulates. We found that bycatch data underestimated bharal density compared to the double-observer method and the reference minimum population count. Although the estimate from camera-based distance sampling targeting ungulates was not statistically different from the double-observer estimate, the wide confidence interval associated with this method is notable.

Pal et al. (2021) used camera-based distance sampling to estimate bharal density in the Upper Bhagirathi Basin of Uttarakhand, India. They estimated 0.51 \pm SE 0.10 bharal/km², which is lower than our study, but their estimates were relatively imprecise with a high coefficient of variation. Although previous studies have compared the performance of different camera-based methods to estimate ungulate numbers (Palencia et al., 2021, 2022), we believe our comparison with estimates from a field-based survey is novel, especially the inclusion of ungulate bycatch data from a survey designed to estimate the size of a predator population.

It is possible that camera-based distance sampling may have underestimated bharal population size (from ungulate bycatch data) or been imprecise (from cameras deployed to survey bharal) because of practical constraints, such as differences between the theoretical and actual angle of each camera with respect to the ground (Corlatti et al., 2020). If the movement sensors are less sensitive to movement near the edges of the camera's field of view, this can result in underestimates, particularly when using photos rather than videos. Our analysis demonstrated that there was generally no bias in camera-trap deployment, so we conclude that the underestimate in the size of the bharal population calculated from the bycatch data was probably a result of the cameras being placed in microhabitats suitable for snow leopards but avoided by bharal. Further research is needed to confirm this.

Sampling accuracy could be improved by increasing the number of cameras (Howe et al., 2017; Cappelle et al., 2021) but there are important logistical considerations (Table 1). Likewise, although the double-observer estimate was more accurate, we acknowledge the difficulties associated with surveys in extremely rugged or remote areas where access is challenging, ungulates flee from people and experienced observers are crucial (Khanyari et al., 2021; Moheb et al., 2023). It is also possible that the double-observer estimate was similar to the total bharal count (Fig. 3) because the assumption of complete visual coverage was upheld by the experienced field teams (> 13 years survey experience) who located and counted the majority of bharal groups over the two surveys. However, further evaluation is needed.

Finally, we note that camera-based distance sampling gives a density estimate, whereas the double-observer method and the total bharal count provide an estimate of abundance from which density is calculated. We advocate for similar comparative studies for other mountain ungulates to assess the wider application of our findings. We also recognize the value of using ungulate bycatch data from large-scale predator surveys. These surveys are often done on tight budgets, and data on other species can be used to estimate their relative abundance, occupancy and distribution, which maximizes output.

There are other methods of deriving ungulate density estimates from camera-trap data, which we plan to assess in future. These include the Random Encounter Model (REM) and the Random Encounter and Staying Time (REST). We analysed our data using a Random Encounter Model but concluded that the results were unreliable and required better field calibration of parameters such as day range, encounter rate and detection zone (Rowcliffe et al., 2011; Palencia et al., 2022). Palencia et al. (2021) highlighted the mathematical equivalence of camera-based distance sampling and the REST method. We note that it is logistically challenging to uphold the assumption of random camera placement when working in areas such as the trans-Himalaya, which undermines some analyses (Glover-Kapfer et al., 2019).

Beyond the robustness of the methods in terms of the accuracy and precision of the estimate they provide, we also evaluated logistics and practical application. First and foremost, substantial numbers of camera traps are required to improve the precision of density estimates derived from camera-based distance sampling (Cappelle et al., 2019). This method was more costly and labour-intensive because of the type of equipment required and the post-survey image processing time. (Corlatti et al., 2020). Field research is often constrained by tight budgets and limited timelines, and Singh & Milner-Gulland (2011) recommended a monitoring strategy matrix to choose the most appropriate method in any given context. Our comparison of double-observer and camera-trap based distance sampling contributes to this debate.

Overall, our results suggest that double-observer surveys focused on ungulates are a better method for estimating population densities than camera-based distance sampling, either from cameras placed to detect predators (yielding a severe underestimate) or to detect ungulates specifically (giving a reasonable estimate but with much less precision and being more logistically intensive). This may not be the case for other study animals or locations where field surveys might be prohibitively expensive. The team of observers in this study have conducted double-observer surveys in the Upper Spiti Landscape for over a decade (Sharma et al., 2024), and we acknowledge that less experienced observers may impact the robustness of population estimates.

In conclusion, our results are crucial to the Global Snow Leopard and Ecosystem Protection Program and efforts to estimate snow leopard and prey populations in

the countries where snow leopards still survive. We clearly demonstrate that camera traps placed to detect predator populations underestimate prey populations. Encouragingly, we confirm that cameras placed to detect ungulates can provide similar population estimates to robust field surveys (Howe et al., 2017; Harris et al., 2020; Pal et al., 2021; Palencia et al., 2021). We caution against the use of bycatch data from cameras placed to detect snow leopards to estimate wild ungulate densities and emphasize that camera-trap surveys of ungulates must uphold the assumptions for the specific method (Howe et al., 2017; Harris et al., 2020; Palencia et al., 2021). We recommend a collaborative approach to predator and prey surveys that integrates ungulate-specific methodologies to achieve more robust population assessments, particularly when carried out across vast landscapes for rare predators like snow leopards.

Author contributions Study conception: MSK, RP, KS; data collection: MSK; data analysis: RR, DB, CS; writing and revision: all authors.

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Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards. Camera trapping was done in a non-intrusive way, ensuring no flash light during hours of darkness and following the *Oryx* ethical code for camera trapping. No images of people were captured. We conducted this research with permission from the Himachal Pradesh Forest Department (permit number WLM/Research Study/Vol-XIV/4406).

Data availability The data that support the findings of this study are available at doi.org/10.5281/zenodo.17357880

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