NICHE SELECTION AND MESOPREDATOR RELEASE IN HIGH -ALTITUDE ECOSYSTEMS

Mesopredator release and competition of wild and commensal predators

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Wildlife Institute of India

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Summary Report

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SUMMARY

Apex predators, such as snow leopards and Himalayan wolves, play a critical role in maintaining ecosystem balance by regulating mesopredator populations and protecting smaller prey species. However, declines in apex predators, driven by habitat loss, human persecution, and environmental changes, can lead to "mesopredator release," where mesopredators like red foxes and free-ranging dogs experience population explosions. This phenomenon disrupts ecological balance and can significantly alter food web dynamics.

In the cold deserts of the Himalayas, this issue is compounded by anthropogenic influences. Free-ranging dogs, sustained by human-provided resources like livestock waste and garbage, have expanded their range and ecological impact. This expansion disrupts existing predator-prey relationships, increases competition for resources, and poses threats to native wildlife including both native predators and prey species.

The proposed research aims to investigate the dynamics within the carnivore guild in the Spiti Valley, focusing on how resource availability and anthropogenic influences drive carnivore community dynamics. The study area is located in in Himachal Pradesh's Lahaul–Spiti district, bordered by Ladakh to the north, the greater Himalayas to the south and west, and Tibet to the east, with elevations between 3,600 and 6,700 m. The Cold Desert Biosphere Reserve encompasses the entire Spiti Valley, known for its drastic climate differences from dry summers with temperatures up to 30 ° C to harsh, freezing winters reaching -40°C. The vegetation is predominantly alpine scrub and dry alpine steppe. The local, predominantly tribal communities practice agro-pastoralism, growing hardy crops and managing livestock, including yaks and sheep. Climate change poses significant threats to their traditional livelihoods and the valley’s fragile ecosystem.

We chose five intensive study sites in the Spiti Valley, varying in anthropogenic impact, predator-prey dynamics, and dog presence. Chandratal is a popular hiking destination with a sanctuary and a Ramsar-designated lake. Kibber hosts major settlements like Kaza, with increased tourism leading to an increase in dog populations. Pin, encompasses the Pin and Parahio rivers within the Pin Valley National Park, its buffer zone inhabited by 13 villages excluding summer settlements. Mane is a trek base, and Gue restricts tourism near the India-China border.

The native predator guild of the valley includes snow leopards (*Panthera uncia*), Himalayan wolves (*Canis lupus chanco*), and red foxes (*Vulpes vulpes*), with free-ranging dogs (*Canis lupus familiaris*) as introduced predators. Snow leopards and Himalayan wolves are both classified as vulnerable by the IUCN Red List and face significant threats from habitat degradation, human conflict, and competition with free-ranging dogs. The snow leopard, a flagship species for conservation in Asia's highlands, is particularly affected by these pressures. Himalayan wolves, also classified as vulnerable, face additional threats such as hybridization with dogs. The red fox, categorized as Least Concern, is the most widespread wild carnivore in the region, though it is less studied due to its elusive behavior. Free-ranging dogs, while not native, are a major threat to both livestock and wildlife in the valley, causing more livestock losses than snow leopards and wolves and competing with native red foxes for resources.

By examining how snow leopards, Himalayan wolves, red foxes, and free-ranging dogs partition resources and compete within their guild across spatial, dietary, and temporal dimensions, the study aims to understand the intricate dynamics of carnivore interactions. This will provide insights into how human-altered landscapes influence carnivore niche spaces. The research is crucial for understanding the ecological consequences of species interactions in human-influenced ecosystems and developing effective conservation strategies for the fragile Himalayan environment.

To study spatiotemporal interactions among top predators (snow leopards, Himalayan wolves) and mesopredators (red foxes, dogs), we deployed 205 camera traps across five study sites in Spiti Valley. In two sessions (August 2021-April 2022 and May-August 2022), cameras were placed in a 1x1 km grid, with specific distributions in Chandratal, Kibber, Pin Valley, Mane, and Gue. An additional session involved a 5x5 km grid to assess broader landscape impacts. Camera traps were placed on trails or near carnivore signs, with images identified using field guides and trapping efforts measured in camera days. Scat samples from carnivores were collected during trail surveys and camera trap deployments, with distinguishing features noted to minimize misidentification. For dog population estimation, we surveyed villages by walking trails and photographing dogs, identifying individuals by markings. GPS telemetry was used to track red foxes, with three individuals fitted with collars to monitor movement patterns. Collars recorded GPS fixes at 4-hour intervals, though technical issues and rugged terrain limited some data collection.

In our analysis of spatial patterns and interactions among predators, we used a multispecies occupancy model to account for imperfect detection, evaluating hypotheses related to habitat, prey, anthropogenic influences, and competition. Camera trap data were formatted into detection history matrices and analyzed using the camtrapR package in R, focusing on pairwise interactions between four predator species. We incorporated habitat, prey, and anthropogenic impact covariates and assessed their effects through a two-step model selection process based on AICc. Co-occurrence was analyzed using Pianka’s niche overlap index and probabilistic models to determine interaction types. Temporal overlap was assessed through kernel density estimation, with statistical comparisons made using the Mardia–Watson–Wheeler test. Diet analysis involved scat sample examination and integration of published data to evaluate niche overlap using Pianka's index and randomization tests. For population estimates, we utilized SECR methods for both dogs and red foxes, considering detection parameters. Home range sizes for red foxes were estimated using MCP and KDE methods. We compared RAIs of top and mesopredators to understand mesopredator release dynamics in the region

The study reveals positive associations between red fox occupancy and the presence of other predators, highlighting the significance of prey, elevation, and distance to settlements covariates. This positive spatial association between red foxes and top predators, suggests potential facilitation driven by red foxes' carrion scavenging behavior. Further, our study found both negative and positive spatial associations among dogs, snow leopards, and wolves, depending on covariates. Positive spatial associations found between dogs and native carnivores, raise concerns about disease transmission and hybridization risks in case of Himalayan wolves. However, evidence of mesopredator suppression was also observed, particularly in areas where high predator abundance constrains the distribution and resource access of red foxes.

Significant dietary overlap among carnivores was detected, primarily due to their shared reliance on domestic animals. This overlap increases competition for limited resources, prompting carnivores to partition their niches through variations in activity patterns. For instance, red foxes primarily exhibit nocturnal behavior, whereas snow leopards are crepuscular, demonstrating how temporal separation can reduce direct competition. Understanding these dietary dynamics is crucial for managing human-carnivore conflicts and conserving vulnerable species.

The study highlights the increasing presence of free-ranging dogs in the Spiti Valley, which poses significant threats for the survival and ecological balance of native carnivores. As these dogs establish themselves in the landscape, they directly compete with native carnivores for food resources, which can lead to a decline in prey availability for species like snow leopards and anthropogenic subsidies for species like red foxes. This competition can exacerbate existing pressures on these carnivores, making it more difficult for them to access the food they need to thrive. The tendency of these dogs to congregate near human settlements—where they often thrive on waste and food scraps—exacerbates these issues. This reliance on human refuse not only boosts dog populations but also alters the behavior and movement patterns of native carnivores, forcing them to adapt to an increasingly competitive and anthropogenic landscape. Thus, effective management of free-ranging dog populations becomes imperative to mitigating their impact on native wildlife and maintaining ecological balance. Strategies such as sterilization programs, responsible pet ownership education, and improved waste management are crucial to curbing the adverse effects of domestic animals on the region's wildlife.

The research employed Spatially-Explicit Capture-Recapture (SECR) methods to yield reliable density estimates for red fox populations, revealing smaller home ranges in areas with human influence. This finding suggests that the availability of anthropogenic food sources, such as livestock remains and human waste, likely reduces the need for extensive foraging, allowing red foxes to thrive in proximity to human settlements. However, this reliance on human-provided resources also indicates a potential vulnerability, as changes in human practices or resource availability could drastically impact red fox populations. Consequently, understanding the dynamics of resource availability is essential for effective management of mesopredator species like red foxes. Conservation efforts must consider these factors to ensure the long-term survival and ecological roles of native carnivores within the Spiti Valley.

While the study offers valuable insights, it acknowledges limitations such as the constrained camera trap data and variability in dog populations across human settlements, which hinder understanding of carnivore interactions. Future research should focus on collaring multiple individuals of all carnivores to refine the knowledge of fine-scale spatio-temporal interactions. Investigating the effects of introduced mesopredators, like dogs, can also be enhanced by using GPS collars. Long-term studies, particularly during winter—a season of heightened resource scarcity—are essential for understanding competition among carnivores.

Future research should focus on expanding sampling efforts and refining methodologies to gain a more nuanced understanding of the intricate interactions within carnivore communities. By addressing current knowledge gaps, particularly regarding the effects of top predators on mesopredators and the influence of human activities on these dynamics, future studies can inform more effective conservation strategies in this ecologically significant region.

OBJECTIVES AND RESEARCH QUESTIONS

1. To determine niche selection of high-altitude carnivores

Question 1: What is the resource use of Snow leopards, Himalayan wolves, red foxes and free ranging dogs in the trans-Himalayan region?

Question 2: How does resource selection vary between these carnivores across the niche dimensions of space, time and diet.

2. To investigate levels of overlap and influence by high altitude carnivores in terms of mesopredator release or suppression

Question 1: How do interactions amongst intra-guild predators influence top-down effects in terms of mesopredator relative abundance and distribution?

Question 2: How do bottom-up processes such as resources availability influence mesopredator release among the carnivore guild?

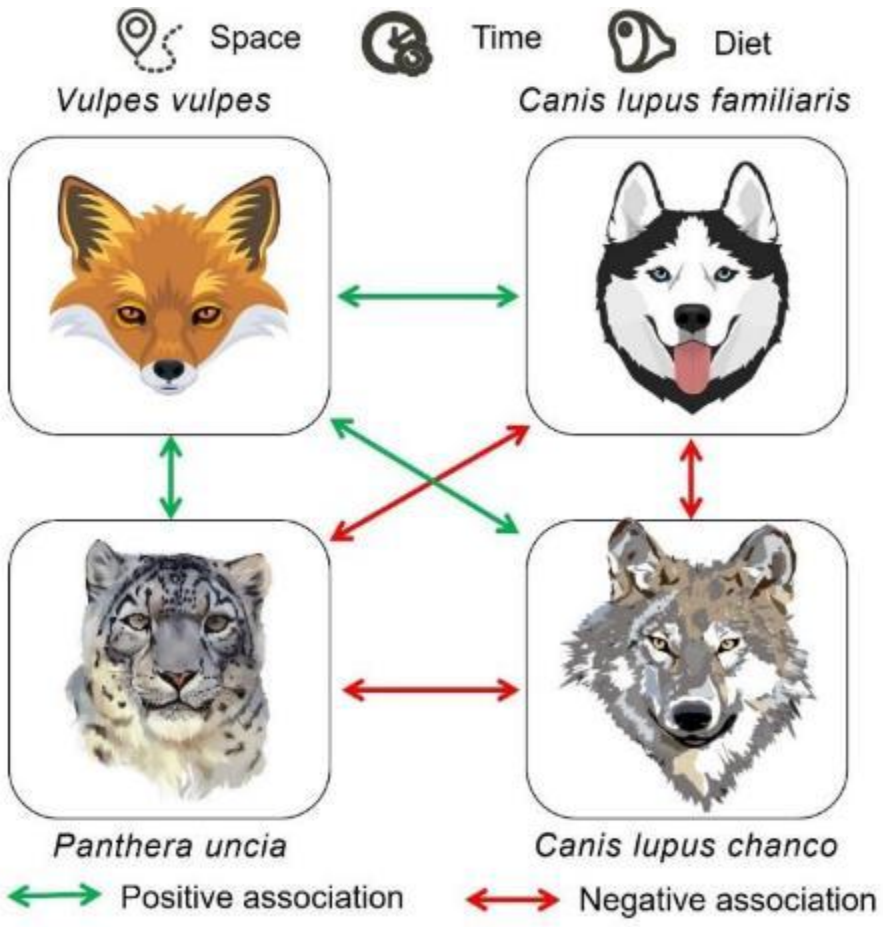

Figure 1.1 Conceptual frame work of association between carnivores (red fox, dog, snow leopard and Himalayan Wolf) in Spiti Valley, H.P.

METHODS

1. Based on extant literature, key informant questionnaire surveys, and sign surveys (Joshi et al., 2020), we selected five intensive study areas in the trans-Himalayan landscape of Spiti valley (Fig 1). The sites differ in terms of the intensity of anthropogenic imprint, predator and prey distribution and abundance, and the presence of domestic, free-ranging, and feral dogs. Table 1 lists the sites, season of camera trapping and major characteristics of these sites.

Table 1. Characteristics of the selected sites and the season when camera trapping was carried across these sites

Site	*Season (Month)*	*Characteristics*
Chandratal	Summer (*Aug- Sept 2021*)	- popular hiking and camping destination - protection status of wildlife sanctuary and a Ramsar site - no permanent settlements - accessible only during summer
Kibber	Winter *(Nov-Dec 2021),* Summer *(May-June 2022)*	- principal settlements of the valley in this area - protection status of wildlife sanctuary - maximum tourism infrastructure and dog population
Pin	Summer *(Sep-Oct 2021),*	- protection status of a national park - four summer settlements in the core area of the park and 3-4 villages in the periphery
Mane	Winter *(Jan-Feb 2022),* Summer *(June-July 2022)*	- the base for treks to the Sopona lake and further towards Manirang Pass - one village and a summer settlement near Sopona lake
Gue	Summer *(June-July 2022)*	- located just kilometers away from the India-China border therefore locals and tourists are restricted from visiting certain areas - a small village with less human imprint

2. To study the spatio-temporal resource use of the top predators (snow leopard, Himalayan wolf) and mesopredators (red fox, dogs) we deployed camera traps in a 1X1 sq. km grid. Camera-trap locations were selected based on accessibility, terrain features, and trails with carnivore signs (Marinho et al., 2018). A single camera with motion sensors was deployed at each location, and a time lag of 2s was set between animal detections. After the completion of one camera-trapping session across three sites, the photographs were examined for images of animals using a field guide (Menon, 2003). The amount of trapping effort required (unit: camera days) was calculated for each camera from when the camera was mounted until the camera was retrieved.

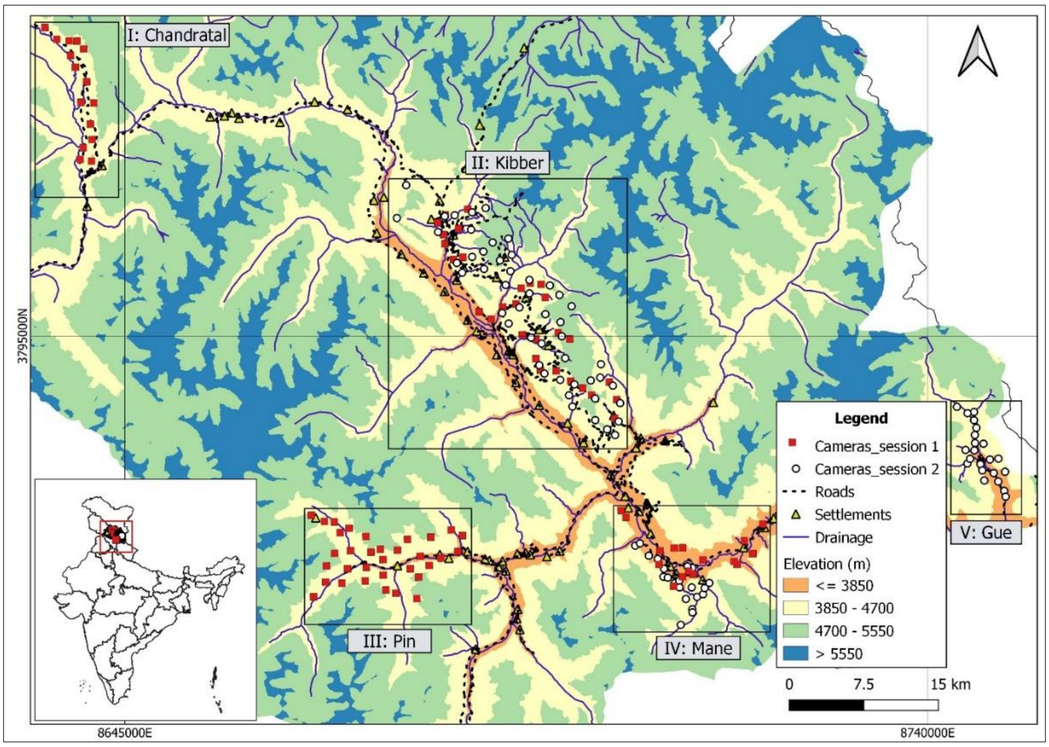

Figure 1. Map depicting intensive study areas in Spiti valley, H.P., India (Camera trapping: session 1: Aug 2021-Jan 2022; session 2: May-Aug 2022)

2.1 We used the multispecies occupancy model (Rota et al., 2016), to access the spatial interaction of dog, red fox, snow leopard, and wolf, while accounting for imperfect detection. As the data was collected using camera trapping, estimates are more analogous to "use" rather than true occupancy (Burton et al., 2015). This model is a generalization of the single-species occupancy model (MacKenzie et al., 2017) that accommodates two or more interacting species. For each of the species, s = 1, …., S at sites I = 1, ..., I, a latent occupancy state (Zi) is included in the modeling framework represented by a sequence of 0/1 values (indicating species absence/presence).

We modeled occupancy using with five covariates based on prior studies (Contardo et al., 2021; Ghoshal, 2011; Murdoch et al., 2016; Rehman et al., 2021). Habitat factors, including elevation (DEM) and Terrain Ruggedness Index (TRI), were selected, and anthropogenic impact was assessed using Distance to roads and settlements. Prey covariate was determined by prey encounter rates calculated through trap success (number of detections of prey species/total camera trap days × 100) (Merson et al., 2020). For red fox, small prey encounter rates (pika and woolly hare) were considered, while large prey encounter rates (Himalayan ibex, blue sheep, and livestock) were considered for dog, snow leopard, and Himalayan wolf. Covariates were averaged for each camera trap grid using QGIS 3.16.14. Detection covariate was trap nights, and all continuous variables were standardized to z scores before analysis. Univariate correlations (r>0.4) were examined using a Pearson correlation matrix, and correlated covariates were dropped (Hooten et al., 2015).

For the multispecies occupancy analysis, we formatted the camera trap data by generating detection histories into matrices of sites i by sampling occasions j, using one week as the resolution for model convergence and precision of estimates using the R package camtrapR (Niedballa et al., 2016). In our analysis, we only considered pairwise interactions between four predators resulting in ten natural parameters being modeled. In total 18 models were run per species pair and we selected the best models by comparing Akaike's information criterion (AIC) for each model (Akaike, 1974; Burnham & Anderson, 2002).We implemented the models using the package ‘unmarked’ in R (Fiske & Chandler, 2011; R Core Team, 2023).

2.2 Spatial overlap among species was assessed using Pianka’s niche overlap index (Pianka, 1973), calculated from the relative abundance index (RAI) of four predator species (Carbone et al., 2001). Utilizing photographic rate as a proxy for abundance, each camera trap station was considered spatially independent. Ranging from 0.0 (no shared habitats) to 1.0 (identical habitat use), the spatial overlap index quantifies habitat overlap between species (Pianka, 1973). Furthermore, we examined species pairs' spatial interactions with two probabilistic models: (1) Probability of lower co-occurrence frequency (Plt), and (2) Probability of higher co-occurrence frequency (Pgt). Plt <0.05 and Pgt <0.05 indicate negative (competitive interaction) and positive co-occurrence (no antagonism) between the two species pairs, respectively (Griffith et al., 2016).

2.3 To determine the activity periods of each species, the date and time printed on the photographs were utilized. We assumed that the number of camera trap records taken at various times was correlated with the daily activity patterns of mammals (Linkie & Ridout, 2011). To maintain statistical independence and reduce bias caused by repeated detections of the same individual, one record of each species per half hour per camera trap site was considered an independent detection, and subsequent records were removed (Carbone et al., 2001). The analysis was performed for the predators with at least ten records. We used kernel density estimation to estimate the overlap coefficient, a quantitative measure ranging from 0 (no overlap) to 1 (identical activity patterns), in the R platform using the overlap package (Ridout & Linkie, 2009). Overlap coefficient (Δ) was defined as the area under the curve that is formed by taking at least two density functions at each time point ranging from 0 (no overlap) to 1 (complete overlap), where 0 implies that the species have no common active period and 1 implies that the activity densities of two species are identical (Schmid & Schmidt, 2006). The precision of this estimator was obtained through 95% confidence interval (CI), as percentile intervals from 999 bootstrap samples (Linkie & Ridout, 2011; Meredith & Ridout, 2016). As the coefficient of overlap is descriptive, we employed the Mardia–Watson–Wheeler (MWW) test (Batschelet, 1981) to statistically compare detection distributions across diel cycles for all predator pairs (Brook et al., 2012). We rejected the null hypothesis of a common distribution when the value of W exceeded the critical value, as indicated by $p < 0.05$ (Pewsey et al., 2013).

3. Scat samples of the study carnivores were collected from the field during the sign survey (trail transects) and opportunistically while walking on trails for deploying the camera traps in Aug 2021– July 2022. Scats of the study carnivores were distinguished in the field based on shape, size, odor, quantity, and signs typical to that of the relative species (Jackson & Hunter, 1996; Menon, 2003; Vanak & Mukherjee, 2008). All of the scat samples were collected in a zip lock bag and were labeled with sample ID, date, GPS location, and habitat characteristics. The scats which had moisture were sun-dried till they were completely dry for storage.

3.1 The scat samples collected were processed in the Animal Biology lab, Dehradun for diet analysis of the carnivores. Initially, the outer layer of each scat sample was removed with a blade, and the processed material was preserved in an Eppendorf tube for subsequent DNA analysis to identify the species. Scat samples were then homogenized and undigested items (hair, bone fragments, hooves, feathers, and claws, chitin remains of insects, seeds, and other plant material) and human-derived materials (cloth, paper, and plastic) were collected in labeled zip lock bags for further identification. After separating various items, samples of 20 hairs from each scat were randomly drawn for prey identification (Jethva & Jhala, 2003; Mukherjee et al., 1994). Slides containing randomly selected hair samples from a specimen were subjected to a Hydrogen peroxide wash, followed by a 6-8 hour immersion in Xylene. Subsequently, these slides were scrutinized under a light microscope to discern the prey identified through medullary hair patterns (Anwar et al., 2012; Oli, 1993).

3.2 We calculated the relative frequency of occurrence (RF) as no. of occurrences of each food type (species) when present/total no. occurrences of all food items ×100 (Shrestha et al., 2018). To calculate food niche overlap between the carnivores, we used Pianka's index, with the formula:

$$O_{jk}=\Sigma P_{ij}\ \Sigma P_{ik}/\ \Sigma P_{ij}^2\ \Sigma P_{ik}^2$$

where O_{jk} is Pianka's index of niche overlap between species j and k, while P_{ij} and P_{ik} are the proportions of use of resource category i by species j and k respectively. We took prey species to be a resource category. Pianka's index varies between 0 (total separation) and 1 (total overlap) (Krebs, 1989; Pianka, 1973). We evaluated if the observed niche overlap significantly deviated from what the null hypothesis predicts which assumes that carnivores independently consume prey species. Using the "ra3" randomization algorithm, a conservative approach that maintains species' niche breadth, we performed 10,000 iterations to assess diet niche overlap with "EcoSimR" package (Gotelli et al., 2015).

4. For dog population estimation, the intensive survey area was divided into 1 × 1 km^2 polygons, their extent representing the average known home range of free-ranging dogs, ~0.72 km^2 (Dürr & Ward, 2014; Pal et al., 1998). Each polygon was sampled on four-five occasions on consecutive days. Existing trails were walked in each polygon, following the same paths each time (Gogoi et al., 2020; Punjabi et al., 2012). Dogs were photographed using an SLR camera and their GPS locations were noted. Individual dogs were identified based on body colour, sex, and natural marks (Punjabi et al., 2012). Individual capture histories for dogs and polygon vertices were used for developing trap files to be used as inputs in SECR analysis (Borchers, 2012) for the estimation of dog abundance using the Polygon search method (Gogoi et al., 2020).

5. For density estimation of red fox, we used Spatially-explicit capture recapture. The identification of individual foxes was established upon various physical characteristics (Plate 2). Predominantly, the key features for identification included the skin patterns on the lower limbs, body morphology, and the tail (Sarmento et al., 2009). A crucial factor was capturing photographs of both flanks of the animal. Despite not employing opposing cameras at each station, the behaviour of foxes facilitated the acquisition of multiple photographs of the same individual from various angles. The identification process, adapted from (Jackson et al., 2005), included initial capture, recapture, and null capture. It involved assessing primary features (distinctive body areas), secondary features (other useful marks), and determining initial capture or recapture based on the comparison of these features.

We estimated population density of red fox using SECR package (Efford, 2023) in R (R Core Team, 2023). SECR models utilise the fact animals have a higher probability to be detected if they spend more time close to detectors. The SECR model needs two parameters: (1) detection probability (g0), and (2) spatial scale at which encounter rates or detection probabilities decrease when animals' activity centres and detectors are located further apart (σ). Although alternative forms of the relationship can be considered, it is often assumed that the form is half-normal (Howe et al., 2022). The model assumptions for simulating data are twofold: first, animals have stable activity centres with no ongoing emigration or immigration, and captures are treated as binary events with 'proximity' as the detector type; second, the detection process is assumed to be a continuous function extending from the activity centres to the point of no capture probability, modelled as a half-normal function. A buffer value four times the sigma was utilized to ensure that individuals with activity centres outside the trap array were included in the density estimation (Borchers & Efford, 2008).

6. Telemetry studies offer a crucial window into the intricate movements and habitat utilization of animals, particularly in challenging environments like the Spiti Valley (Sollmann et al., 2013). In our investigation into the movement patterns of red foxes, we utilized humane trapping methods to collar three individuals for tracking. Employing padded leg-hold traps near the village during twilight hours, we minimized interference from dogs, capitalizing on the nocturnal behavior of the foxes. After capture, we estimated their weight for safe immobilization, administering a combination of combination of Tiletamine Zolazepam-Medetomidine (Muliya et al. 2017). Continuous monitoring of vital signs and oxygen supplementation mitigated the risks associated with high-altitude anesthesia.
Two foxes were equipped with satellite-GPS collars (Litetrack 150 iridium) programmed to record fixes every 4 hours, while one fox was fitted with VHF collar. We estimated the home range sizes of red fox using minimum convex polygon (MCP) and kernel density estimator (KDE), from the ArcMET utilization distribution and range tools (Wall, 2019). Monitoring commenced in September 2023, with one individual still transmitting data. However, technical issues led to the malfunction of one satellite collar within a week, and rugged terrain impeded VHF collar monitoring, limiting our analysis to a single adult female.

7. We computed the relative abundance index (RAI) of the top predators (snow leopard and Himalayan Wolf) and mesopredators (red fox and dog) across all study sites. This was calculated as a total number of independent photographs for each species (A) divided by total trap nights (N) and multiplied by 100.

$$RAI = (A/N) \times 100$$ (Carbone et al., 2001)

The criteria to determine a photographic event (a species occurrence) were (1) consecutive photographs of the same species within 30 minutes were counted as one species occurrence, and (2) different identifiable individuals were treated as a separate occurrence even though they appeared in the same photograph, or the photographs were taken within 30 minutes. The analysis was carried out in a windows-based MS office excel worksheet using the data analysis

RESULTS

1. Details of the number of cameras deployed and total camera days per site have been given in the table below (Table 2). A total of 205 camera traps were deployed for a total of 8087 camera days.

2. In the first session (Winter), the overall trapping effort spanned 3,998 days. This comprised camera trapping activities across four sites: Chandratal (529 days), Kibber (1,355 days), Pin (1,394 days), and Mane (720 days). In session 2 (Summer), the trapping effort spanned to a total of 4121 days. This effort was distributed across three sites, with specific durations for each location: Kibber (2186 days), Mane (945 days), and Gue (990 days) (Table 2).

Table 2 No. of camera traps deployed and total effort across six study sites in Spiti valley

S. No.	*Site*	*Cameras Deployed (session 1, 2)*	*Camera days: total effort (session 1, 2)*
1	Chandratal	15	529
2	Kibber	39, 50	1355, 2186
3	Pin	43, 48	1394
4	Mane	16, 21	720, 945
5	Gue	22	990

2.1 A total of 8119 camera days resulted in 220, 770, 161, and 79 independent captures of dog, red fox, snow leopard, and wolf respectively. Estimated naïve occupancy (i.e., the proportion of sites in which the predators were detected) was 0.3 for dogs, 0.7 for red fox, 0.4 for the snow leopard, and 0.1 for the wolf. According to null models, the detection probabilities of dog, red fox, snow leopard, and Himalayan wolf were 0.1± SE 0.05, 0.5± SE 0.03, 0.2 ± SE 0.04, and 0.2± SE 0.09 respectively. The null model performed better than the models that considered trap nights as detection covariate. The marginal occupancy probabilities of dogs, red foxes, and wolves were primarily influenced by prey encounter rate, with their likelihood of occupancy rising as prey encounter rate increased. Whereas, the marginal occupancy probability of snow leopards was predominantly determined by distance to settlement, with their occupancy probability decreasing as distance from settlement increased.

In the absence of covariates, positive pairwise interactions were observed between red foxes and dogs, and dogs and wolves, while other interactions lacked significance. Prey encounter rate emerged as the primary covariate in explaining the conditional occupancy probability of red foxes with dogs and, to some extent, for snow leopards. The likelihood of red fox occupancy increased with increase in prey encounter rate, conditional on the presence of both these predators. Conditional occupancy of other predator pairs was best explained by habitat covariates. The red fox was likely to occupy a location as the elevation increased given the presence of snow leopard. Both red fox and dogs were likely to co-occur with increasing distance to settlement. Similarly, the probability of a dog occupying a site conditional on snow leopard presence decreased with increasing distance to road but increased with increase in elevation. The likelihood of snow leopard occupying a site given wolf presence also declined with an increase in distance to road, but increased with increasing distance to settlement. Further, given the presence of wolves, the dog's occupancy probability decreased with an increase in distance to roads but increased with increase in distance to settlement (Fig. 2).

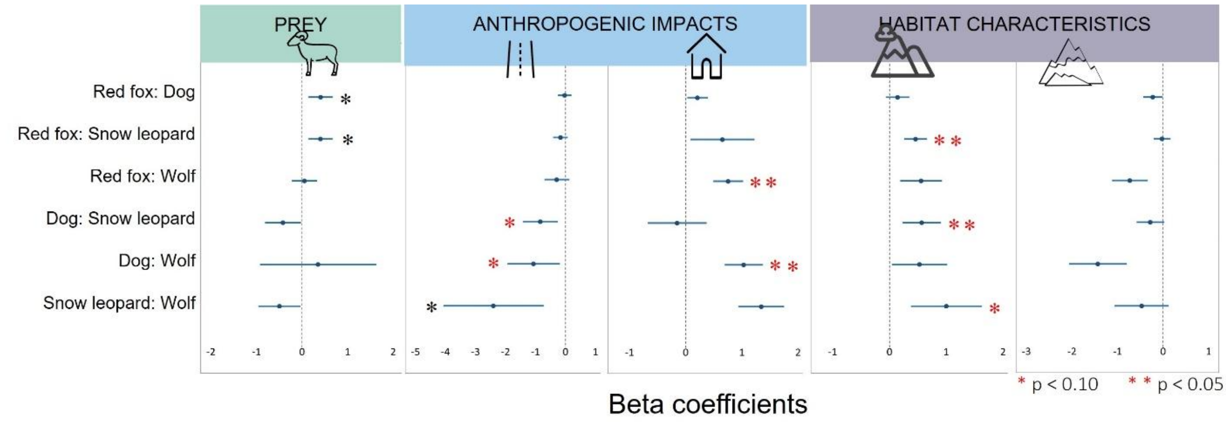

Figure 2 Beta coefficients of prey, anthropogenic and habitat covariates on predator's co-occurrence in the Spiti valley, India. The asterisk indicates the top model covariates for the co-occurrence patterns.

2.2 Spatial overlap ranged from 0.01 (dog and snow leopard) to 0.61 (red fox and wolf). Two species pairs red fox- dog and dog-wolf showed positive co-occurrence, remaining species pairs showed random distribution across the study area (Fig 3, Fig. 7).

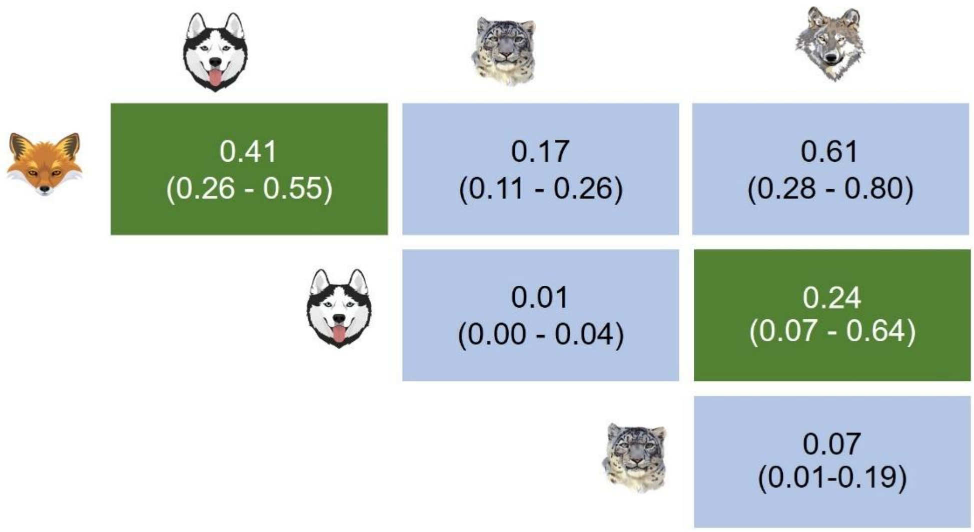

Figure 3 Heat map shows the mean ± CI for spatial overlap index. Green box indicates positive association (P_{gt} <0.0)5 and blue box indicates random species associations (P_{lt} >0.05 and P_{gt} >0.05), for carnivores in Spiti Valley, H.P.

2.3 The study reveals that dogs follow diurnal patterns, while other carnivores exhibit nocturnal or crepuscular activity. Red fox and wolf showed the highest daily activity overlap (Δ = 0.85) and the MWW test shows significant similarity between their diel activity patterns (W = 0.10, p > 0.05). All the other species pairs varied significantly in their activity pattern (Fig. 4, Fig. 7).

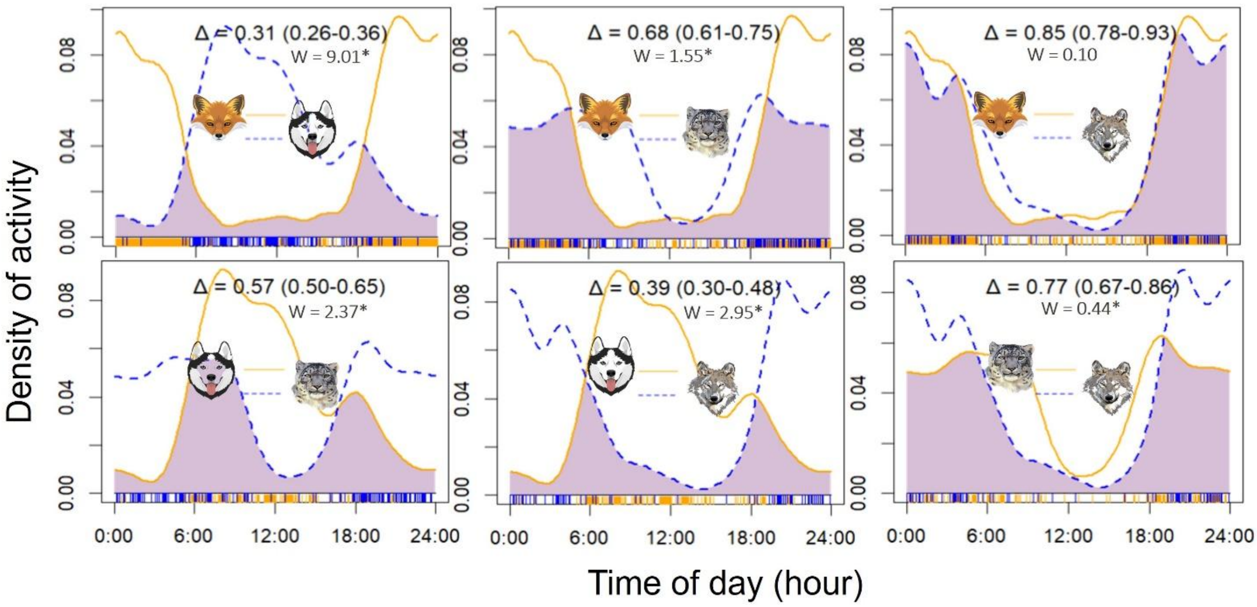

Figure 4 Overlap coefficients of activity patterns and 95% confidence intervals: in brackets () between predator pairs across three study sites. The W value with an asterisk (*) indicates p < 0.05 indicating the two sets of circular distributions came from a different distribution.

3. A total of 1065 carnivore scats were analyzed for this study which includes 279 for dogs, 583 for red fox, 159 for snow leopard and 44 for Himalayan wolf. Additionally, we combined the previous dataset for the present analysis with 118 and 233 scat samples of snow leopard and wolf respectively.

3.1 For determining the relative frequency of various food items in the diets of predators and mesopredators across five study sites we analyzed the remains of 4 domestic and 7 wild species.

3.2 Domestic animals in snow leopard's diet include Cattle (32%), goat (11%), horse/donkey (11%). While contribution of wild prey is 34% with Ibex and Blue sheep contributing to 15% and 7% respectively. A major portion of the wolf's diet was constituted by domestic animals: Cattle (55%), goat (11%) and sheep (10%). Marmot (12%) was the only wild animal that contributed majorly to wolf's diet. Cattle (39%) formed a substantial part of dog diet, followed by items derived from humans (19%), and goat (18%). Further, a major portion of the red fox's diet (37%), consisted mostly of birds (22%) and small mammals namely lagomorphs (7%) and rodents (8%). Cattle (24%) and Goat (8%) also formed a major part of red fox diet (Fig. 5).

3.3 The dietary overlap among predator-pairs was high with values ranging from 0.71 between red fox and wolf to the highest recorded overlap of 0.86 between wolf and snow leopard. The overlap was found to be significant for all species pairs except red fox-snow leopard and red fox- wolf pairs (Fig. 6).

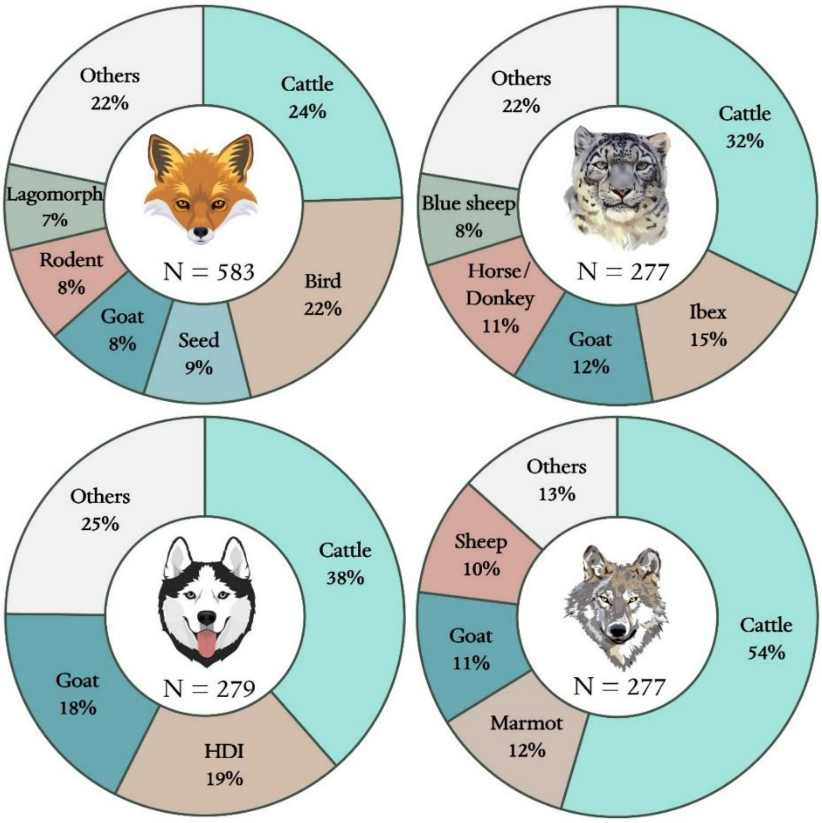

Fig 5. Relative frequency of different food items in the diet of predators in theTrans-Himalayan landscape.

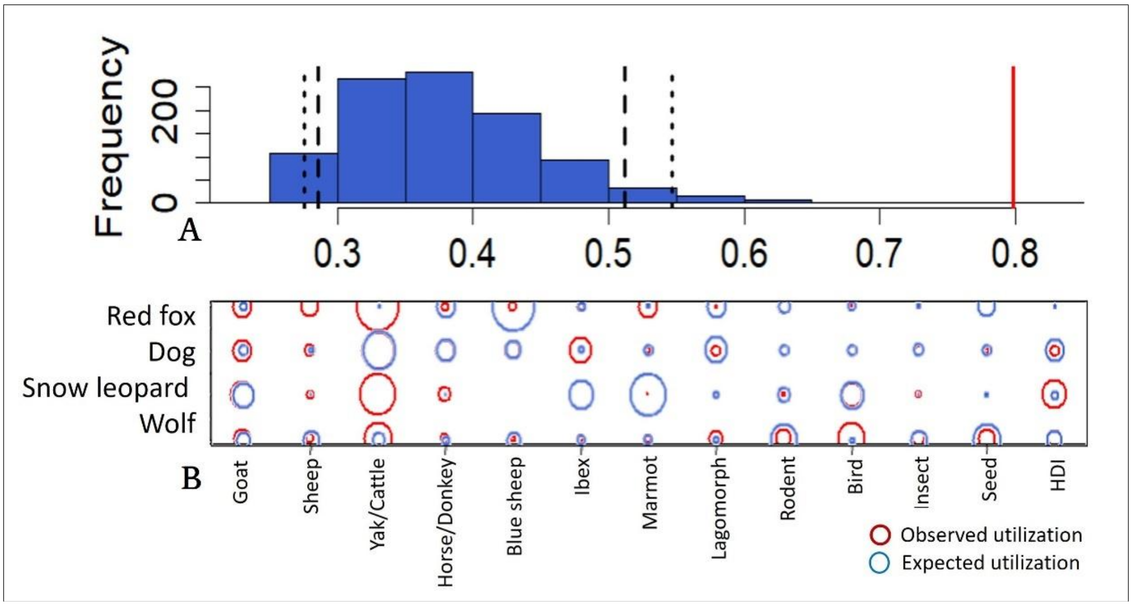

Fig 6. A. Figure displaying histogram (blue bars) of the simulated index values, the observed index value (red vertical line), and the one- and two-tailed 95% confidence intervals (the pairs of black vertical thin-dashed and thick-dashed lines, respectively). B. Comparative dietary niche of the red fox, dog, snow leopard and the wolf (Pianka's mean observed index = 0.79 simulated mean = 0.37; p = 0.002). Larger circles represent relatively higher utilization of the food item.

4. The estimated dog populations and densities across the surveyed villages of Spiti Valley reveal significant variability. The highest population is recorded in Kibber, with 60 ± 3 dogs (95% CI: 56-70), while the lowest population is in Langza, with only 11 ± 4 dogs (95% CI: 8-30). Villages like Mane and Sagnam, Pin also show relatively small populations, with 14 ± 3 and 23 ± 3 dogs respectively. On the other hand, Chicham, with 53 ± 5 dogs (95% CI: 47-66), and Kee, with 32 ± 4 dogs (95% CI: 27-45), represent moderate population sizes. Unique captures range from 7 in Langza to 53 in Kibber, indicating varied detection efforts or different levels of dog detectability across the villages.

   Dog density also varies substantially, with the highest density found in Lidang, at 59 ± 13 dogs per km², followed closely by Kee (56 ± 12 dogs per km²) and Kibber (54 ± 8 dogs per km²). In contrast, the lowest densities are observed in Mane and Sagnam, Pin, both at 12 dogs per km², despite differences in population size. Langza has a slightly higher density of 17 ± 8 dogs per km² but remains on the lower end of the spectrum. Shego, with 22 ± 4 dogs, reports a moderate density of 38 ± 10 dogs per km², while Chicham has a density of 50 ± 8 dogs per km² (Table 3).

Table 3 Village-specific polygon search and SECR-based population and density estimates of dogs with 95% confidence intervals (CI) at three intensive study sites in Spiti Valley, Himachal Pradesh, India [Sigma (σ) = spatial scale of animal movement also an index of home range size; lambda (λ), the per capita detection probability in per unit effort].

Site	**Village**	**model**	**N±SE**	**95%CI**	**Lambda (λ)**	**Sigma** (σ) in meters	**Unique captures**	**Density** (per km²)
Kibber	Chicham	mod.h2	53±5	47-66	0.43±0.06	26	42	50±8
	Kibber	mod.h2	60±3	56-70	0.56±0.06	60	53	54±8
	Kee	mod.h2	32±4	27-45	0.58±0.10	53	24	56±12
	Langza	mod.0	11±4	8 to 30	0.49±0.24	48	7	17±8
	Lidang	mod.h2	28±3	25-39	0.62±0.10	11	24	59±13
	Shego	mod.h2	22±4	19-36	0.56±0.13	403	17	38±10
Mane	Mane	mod.0	14±3	11 to 27	0.65±0.22	79	10	12±04
Pin	Sagnam	mod.0	23±3	20-32	0.62±0.02	125	19	12±03

The spatial scale of movement (σ) ranges from 11 m in Lidang to 403 m in Shego, indicating large differences in home range sizes. Villages like Kibber (60 m) and Kee (53 m) show intermediate movement ranges. Detection probability (λ) varies from 0.43 ± 0.06 in Chicham to as high as 0.65 ± 0.22 in Mane. Langza, despite its small population and low density, has a moderate detection probability of 0.49 ± 0.24.

In most villages (Chicham, Kibber, Kee, Lidang, and Shego), mod.h2 was the best model, where detection probability (λ) was held constant across all individuals, while σ (spatial scale of movement) was allowed to vary between groups. In contrast, for villages like Langza, Mane, and Sagnam, Pin, mod.0 was the top model, where both detection probability and spatial scale of movement were assumed to be uniform across individuals, regardless of group-specific factors (Table 6.6).

The population estimates for six villages in the Spiti Valley were analyzed for the years 2013 and 2022. Notably, Kibber exhibited the largest increase, with its population rising from 18 in

2013 to 60 in 2022, reflecting a remarkable increase of 233% over the nine-year period. Similarly, Chicham showed a significant rise from 8 to 53, resulting in a 563% increase. Other villages also experienced growth, with Kee's population increasing from 11 to 32 (a 191% increase) and Lidang's population rising from 15 to 28 (an increase of 87%). Langza and Shego had smaller population changes, with Langza's estimate growing from 3 to 11 (an increase of 267%) and Shego's increasing from 10 to 22 (a 120% increase). The standard errors (SE) associated with these estimates indicate varying levels of precision, with Shego having the highest SE in 2013 at 8, reflecting greater uncertainty in earlier population estimates (Fig 7).

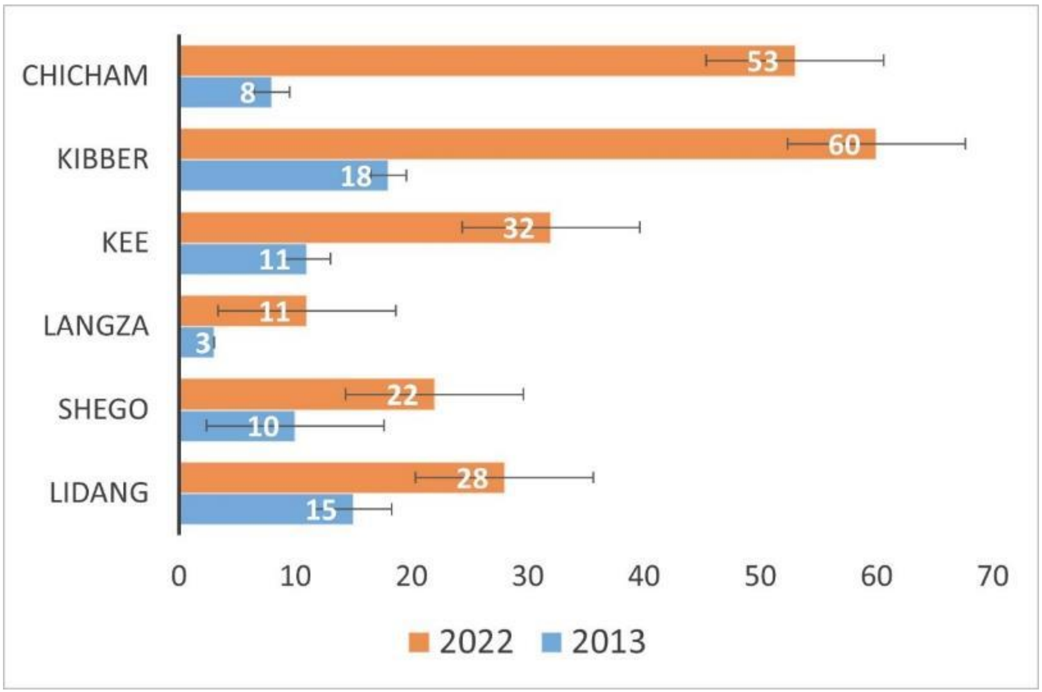

Fig 7 Comparison of dog population estimates in 2013 and 2022 across six villages. The population estimates for 2022 show an overall increase in each village compared to 2013, with the standard errors (SE) for both years represented by error bars. The most significant increase is observed in Chicham and Kibber.

In the smaller villages where the polygon search method could not be conducted, the naïve population estimates reveal modest changes in dog numbers from 2013 to 2022. For instance, Hikkim-Komic saw an increase from 2 to 4 dogs, while Lara experienced a slight rise from 2 to 3 dogs. Conversely, Demul and Gete maintained stable populations at 2 and 1 dog, respectively, and Tashigang reported no dogs in either year. These estimates highlight the variability and stability in dog populations across these smaller settlements.

5. We identified a total of 15, 22 and 28 individual red foxes from Chandratal, Kibber and Pin respectively. The density estimates were 20 individuals per 100 km^2 in Chandratal; 30 individuals per 100 km^2 in Kibber and 21 individuals per 100 km^2 in Pin respectively (Table 4).

Table 4: Red fox (*Vulpes vulpes*) density [D = individuals per km^2; mean±SE (CV)] and maximum likelihood spatial capture–recapture parameter estimates (σ ±SE) in three study sites of Spiti valley, H.P. Parameter estimate g0 of 0.02±0.01 remained constant across the entire analysis.

	Density	*SE*	*Sigma*	*SE*	*CV*
Chandratal	0.20	0.06	0.90	0.14	0.32
Kibber	0.30	0.09	0.53	0.08	0.23
Pin	0.21	0.04	0.65	0.05	0.20
Mane	0.31	0.08	0.54	0.06	0.26
Gue	0.46	0.11	0.76	0.08	0.24

6. The dataset collected from a single female red fox, which consistently transmitted GPS signals, consisted of 2099 GPS fixes. Estimated home range sizes by minimum convex polygon (95% MCP) was 2.05 km^2 with the core area of 0.82 km^2 (50% MCP). Estimated home range sizes by kernel density estimate (KDE) was 1.9 km^2 (95% FKDE) and 0.20 km^2 (50% FKDE) respectively (Fig 8).

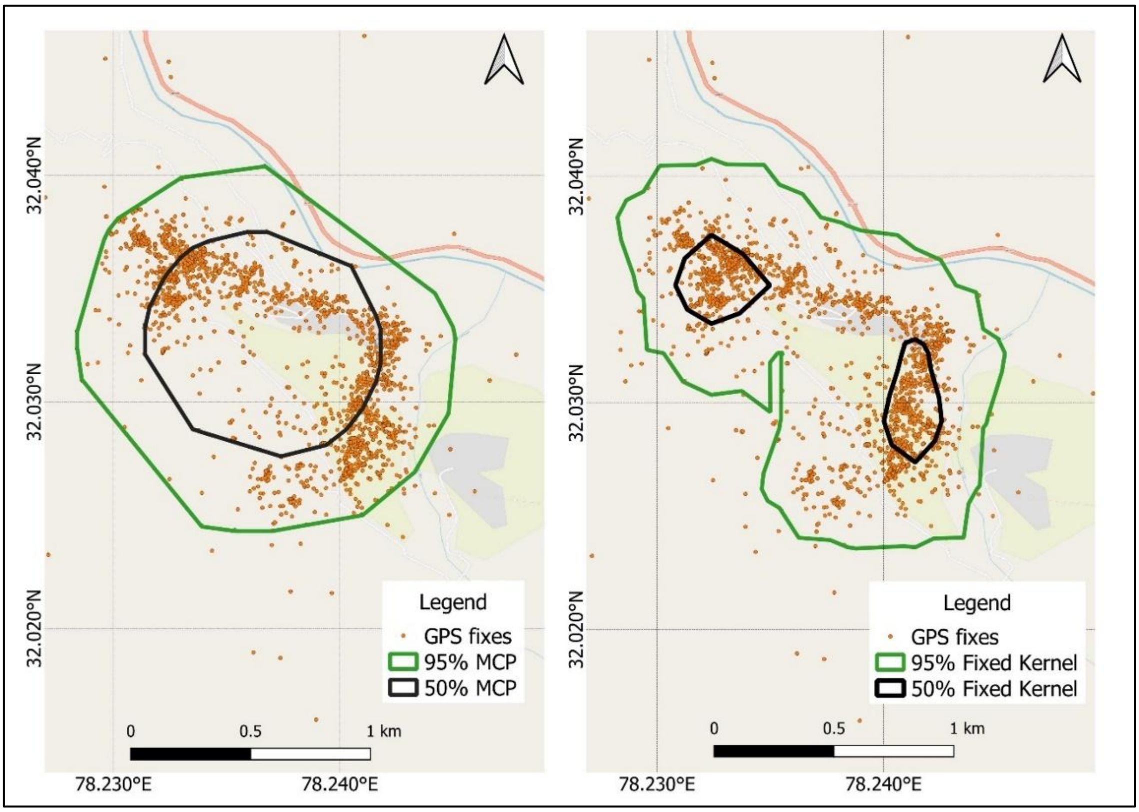

Fig 8. A. 50% and 95% minimum convex polygon (MCP) home ranges of female collared red fox at Spiti Valley. B. Map showing Fixed Kernel Density (FKD) estimate of spatial use of female collared red fox in Spiti Valley.

7. Among the three study areas, Kibber exhibited the highest Relative Abundance Index (RAI) for the apex predator, the Snow leopard (4.4), while Mane had the highest RAI for Wolves (4.8). Further, the RAI for the red fox, a native mesopredator in our study was highest in Pin (12.7), followed by Mane (12.1), and Chandratal (10.8). Dogs exhibited the highest RAI in Chandratal (5.6), followed by Gue (3.6) and Kibber (1.4) (Fig 9).

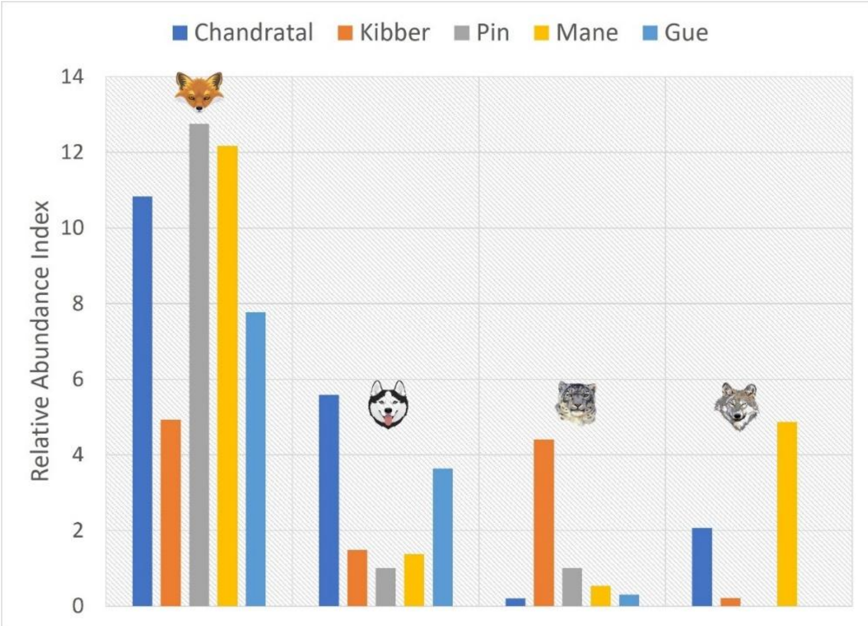

Fig 9. Relative abundance index of top- predators and meso-predators in Spiti Valley, H.P

KEY FINDINGS OF THE RESEARCH PROJECT

1. This study contributes to the growing body of research on carnivore ecology in human-altered landscapes, emphasizing the importance of integrating the influence of human activities and associated species (e.g. domestic animals) on niche selection and resource partitioning among native carnivores. Our study underscores the importance of considering all three critical niche axes—spatial, temporal, and dietary—simultaneously to comprehensively understand carnivore community dynamics.

2. We found positive associations between red fox occupancy and the presence of other predators, highlighting the significance of prey, habitat characterstics, and anthopogenic pressures. This positive spatial association between red foxes and top predators, suggests potential mesopredator facilitation driven by red foxes' opportunist and carrion scavenging behavior. Further, our study found positive spatial associations of dogs with snow leopards and wolves raising concerns about disease transmission and added risk of hybridization in the case of Himalayan wolves.

3. High dietary overlap among carnivores was found, primarily due to their shared reliance on domestic animals implying competition for limited dietary resources. To reduce competition stemming from their shared diets, carnivores partition their niche along at least one axis (Fig 10). Managing livestock and protecting critical habitats while maintaining a healthy prey base are essential to reduce conflicts and support the coexistence and natural interactions of high-altitude carnivores reliant on domestic animals.

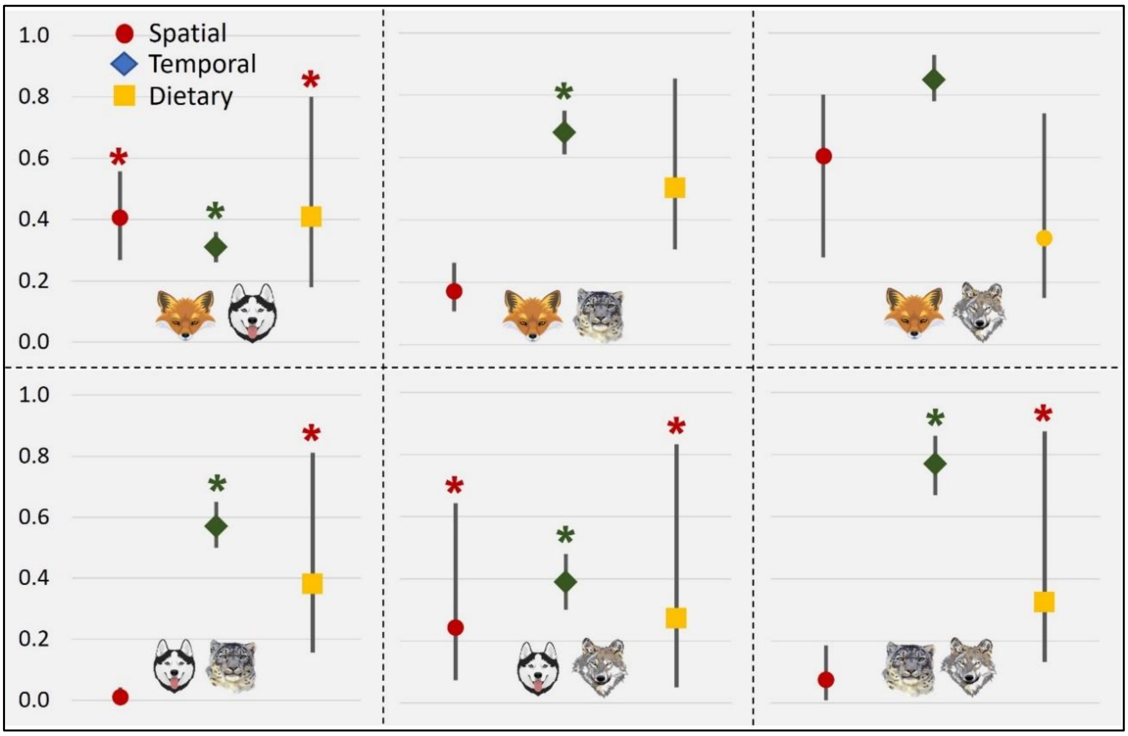

Fig 10. Overlap coefficients (Bootstrap mean ± CI) of spatial, temporal and dietary niche overlaps between carnivores in Spiti Valley, H.P., India. Red asterisk shows significant positive spatial association and significant diet overlaps while the green asterisk shows significant dissimilarity between their temporal activity pattern.

4. We found a notable increase in dog populations across sampled villages, which intensifies competition and poses threats to native carnivores.

5. We have used the SECR method of density estimation of the red fox for the first time to obtain a reliable estimate of abundance, which establishes a baseline and can be useful for monitoring changes in fox abundance in the future.

6. This is the first study in Spiti to collar red fox. Smaller home range of our collared individual which is near human settlements suggest reliance on anthropogenic subsidies (Rotem et al., 2011, Main et al., 2020), highlighting the role of bottom-up processes like resource availability in mesopredator release. Understanding a species movement and home range sizes is crucial for prioritizing conservation areas and informing ecosystem and landscape management. Given the significant variation in home range sizes among individuals (Reshamwala et al. 2022), we recommend collaring more individuals of red foxes and coexisting carnivores across a gradient of disturbance in the near future.

7. Due to limited camera trap photo-captures and absence of a uniform method for density estimation of all carnivores, we used Relative abundance indices to examine the relationship between top predators (snow leopards and wolves) and mesopredators (red foxes and dogs). Negative correlations suggest some form of top-down suppression, with sites like Kibber showing high snow leopard abundance and low red fox abundance. However, low dog abundances in Kibber may result from insufficient camera traps sampling near settlements. Studying mesopredator release or suppression is challenging due to multifaceted interactions, spatial and temporal variability, and indirect effects, compounded by human influence. Despite these challenges, understanding these dynamics is crucial for effective ecosystem management and biodiversity conservation.

ACTION POINTS FOR IMPLEMENTATION & MANAGEMENT IMPLICATIONS

The findings of this study underscore the urgent need for targeted conservation strategies to mitigate human-induced pressures on Spiti Valley's carnivore guild. The increasing presence of free-ranging dogs, driven by anthropogenic subsidies, poses significant ecological threats by competing with native predators, disrupting food webs, and facilitating disease transmission. Simultaneously, the reliance of native carnivores on domestic livestock highlights the importance of managing prey availability and human-wildlife interactions to ensure coexistence. To address these challenges, a multifaceted approach integrating free-ranging dog management, habitat protection, conflict mitigation, long-term research, and policy interventions is crucial. By implementing sterilization programs, improving waste management, strengthening predator protection, supporting community-led conservation efforts, and enhancing scientific monitoring, we can work toward a sustainable balance between wildlife conservation and local livelihoods. These measures will not only safeguard Spiti's apex predators and mesopredators but also maintain the fragile ecological equilibrium of this high-altitude ecosystem.

1. Free-Ranging Dog Management

Sterilization & Vaccination Programs

- Establish a sustained sterilization and vaccination program targeting free-ranging dogs, with a focus on high-conflict areas like Kibber and Mane.
- Engage local veterinarians, wildlife officials, and NGOs to ensure continuous and large-scale implementation.
- Prioritize the vaccination of dogs against canine distemper virus (CDV) and rabies, which pose risks to native carnivores like wolves and snow leopards.
- Conduct regular health screenings for free-ranging dogs to track disease transmission risks to wildlife.

Responsible Pet Ownership Campaigns

- Develop and distribute educational materials in local languages to increase awareness among residents about the ecological impact of stray dogs.
- Implement community meetings and workshops in villages to discuss the dangers of dog abandonment and encourage responsible pet care.
- Work with tourism operators to create guidelines discouraging the feeding of stray dogs by visitors, as it fuels their population growth.

Improved Waste Management

- Install secure garbage bins and waste collection points in villages, monasteries, and tourist sites to prevent dogs from scavenging food waste.
- Implement strict waste disposal protocols in trekking campsites and tourism lodges to minimize food subsidies that sustain dog populations.
- Work with local municipalities and conservation groups to establish waste segregation and composting initiatives that reduce organic waste.

Targeted Dog Control Measures in Key Wildlife Areas

- Identify and designate "high-risk" zones where free-ranging dogs threaten wildlife and implement strict dog population control measures there.

- Explore relocation or shelter-based solutions for stray dogs found in core wildlife habitats.
- Train local wildlife rangers in humane dog deterrence techniques to minimize predation pressure on native carnivores.

2. Carnivore Conservation & Habitat Protection

Strengthen Protection in Key Predator Habitats

- Map and designate high-priority snow leopard and wolf habitats within Spiti Valley for enhanced conservation efforts.
- Establish buffer zones around critical areas like Kibber Wildlife Sanctuary and Pin Valley National Park to regulate human activities that impact predator-prey dynamics.
- Strengthen wildlife protection laws to reduce habitat encroachment, unregulated tourism, and retaliatory killings of predators.

Prey Base Management

- Implement rangeland restoration projects to improve forage availability for wild prey species, reducing their competition with livestock.
- Promote rotational grazing practices among pastoralists to prevent overgrazing and maintain a sustainable wild prey population.

Corridor Protection & Anti-Poaching Efforts

- Identify and protect key wildlife movement corridors to ensure uninterrupted dispersal routes for large carnivores.
- Deploy camera traps and patrolling teams in known poaching hotspots to monitor human-wildlife interactions and detect illegal activities.

3. Human-Wildlife Conflict Mitigation

Community-Based Livestock Protection

- Introduce predator-proof livestock enclosures made with reinforced fencing and night shelters to reduce predation losses.
- Train and equip local herders with non-lethal predator deterrents, such as sound-based alarms or guard animals.
- Establish early-warning systems using camera traps and radio telemetry to alert villagers of predator presence near settlements.

Compensation & Insurance Schemes

- Expand livestock compensation programs to ensure herders receive timely and fair payments for predator-related losses.
- Develop a subsidized insurance scheme in collaboration with the state government and conservation organizations to provide long-term financial security for pastoralists.
- Increase transparency in the verification and claims process to ensure herders trust and participate in compensation initiatives.

Livelihood Diversification for Communities

- Promote ecotourism initiatives that provide alternative income sources for villagers while reducing dependency on livestock grazing.
- Support handicraft and agro-based industries (e.g., organic farming, yak wool weaving) to enhance financial stability for local communities.

- Provide training programs for sustainable tourism operators, emphasizing low-impact activities like wildlife photography and guided treks.

4. Monitoring & Research Expansion

Long-Term GPS Tracking of Carnivores

- Expand collaring efforts for red foxes, snow leopards, and wolves to track movement patterns across different disturbance levels.
- Establish partnerships with universities and research institutions to support long-term ecological monitoring.
- Use GPS data to refine species distribution models and inform conservation zoning plans.

Seasonol Monitoring

- Conduct camera trapping and scat analysis surveys during winter to understand seasonal resource constraints and predator competition.
- Investigate snow leopard and wolf activity patterns during peak livestock grazing seasons to assess human-wildlife interactions.

5. Policy & Conservation Planning

Integrate Findings into Local & State Wildlife Policies

- Collaborate with Himachal Pradesh Forest Department and Ministry of Environment, Forest & Climate Change (MoEFCC) to incorporate research findings into regional conservation policies.
- Advocate for the inclusion of dog population control strategies in wildlife management plans for Spiti Valley.

Collaborate with Local Governance & NGOs

- Engage with Gram Panchayats, local monasteries, and community leaders to implement conservation initiatives at the grassroots level.
- Partner with wildlife NGOs and research institutions to mobilize funding and expertise for long-term carnivore monitoring projects.
- Organize stakeholder meetings with conservationists, policymakers, and community representatives to align conservation goals with local development needs.

Promote Sustainable Tourism Practices

- Develop and enforce eco-tourism guidelines for Spiti Valley that regulate visitor activities near critical wildlife habitats.
- Introduce a tourist education program to reduce human-wildlife conflicts, particularly regarding feeding stray dogs and waste disposal.
- Implement entry restrictions in ecologically sensitive zones, such as Chandratal, to minimize human-induced disturbances.

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