



Original research article

Habitat overlap and interspecific competition between snow leopards and leopards in the Central Himalayas of Nepal

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ABSTRACT

Traditionally, leopards (*Panthera pardus*) and snow leopards (*P. uncia*) occupy distinct habitats. This study explored the coexistence of snow leopards and leopards within the Gaurishankar Conservation Area in Lapchi Valley, Nepal. Both leopard species are crucial for ecosystem stability as apex predators. Camera trapping data from 2018 to 2023 confirmed twenty species of wild mammals and two species of domesticated livestock in Lapchi Valley, where snow leopards have strong spatio-temporal overlap ($\Delta=0.74$) with leopards. Snow leopards exhibited distinct temporal patterns before and after the leopards' arrival in the study area. Generalized Linear Mixed Effect Models (GLMM) revealed seasonal and prey-type associations with leopard presence, highlighting the snow leopards' preference for cold season and wild prey. Leopards, however, did not show a significant seasonal preference. The findings highlight Lapchi Valley's ecological richness as well as the need for comprehensive conservation strategies. The record of spatial and temporal overlap between the leopards and snow leopards provides important insights into the behavioral dynamics of apex predators and the need for targeted biodiversity conservation in the face of changing ecosystems. The study emphasizes the valley's transboundary significance, calling for collaborative efforts between Nepal and China to help promote effective conservation management. Lapchi Valley's isolation, traditional and religious importance, and recent infrastructure developments further impact the conservation challenges.

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1. Introduction

Apex predators play a pivotal role in maintaining the health and balance of ecosystems through both direct predation and indirect behavioral effects on their prey (Ripple et al., 2014; Van Cleave et al., 2018). Among the apex predators, leopards (*Panthera pardus*) and snow leopards (*P. uncia*) are both categorized as Vulnerable by the International Union for Conservation of Nature (IUCN) Red List with decreasing populations (McCarthy et al., 2017; Stein et al., 2023). Both species are critical for ecosystem dynamics in various habitats across Asia. They have traditionally occupied distinct ecological niches to minimize direct competition in mountainous areas. The snow leopards typically prefer cold, rugged terrain of alpine ranges at higher elevations while leopards are usually found in a forest habitat (Lovari et al., 2013a).

Leopards, in particular, show considerable versatility in their habitat use, ranging from tropical to sub-tropical forests. Climate change, however, is causing a rise in the upper limits of forests on mountains (Moiseev et al., 2010; Mainali et al., 2015; Tiwari et al., 2017). As tree lines shift upwards, along with habitat fragmentation, suitable habitat for snow leopards has decreased, particularly in the southern Himalayas (Forrest et al., 2012; Lovari et al., 2013b; Farrington and Li, 2024), an area where both leopard species are reported to coexist (Buzzard et al., 2017; Chetri et al., 2023). The result is an expansion of habitat for leopards and a considerable reduction in habitat for snow leopards (Li et al., 2020) which, in turn, may lead to unfavorable consequences for the long-term conservation of snow leopards due to increasing competition with the larger leopards. The competition for resources, specifically prey and habitat, between these two apex predators in a shared ecosystem can alter the trophic cascade (Estes et al., 2011). The extent and scale of this trophic cascade will depend on several key variables such as the composition and abundance of prey species, spatial availability, and the adaptive capacity of smaller predators (Lovari et al., 2015). Resource exploitation and behavioral disruption, particularly through interspecific killing and kleptoparasitism, are examples of competitive behavior among carnivores (Palomares and Caro, 1999; Donadio and Buskirk, 2006) that might also occur between these two felines.

Overlap in habitat use by snow leopards and leopards has been documented in several areas. Both snow leopards and leopards have been photographed at the same locations in the western Himalaya of India (Pal et al., 2022) as well as in various regions of China, such

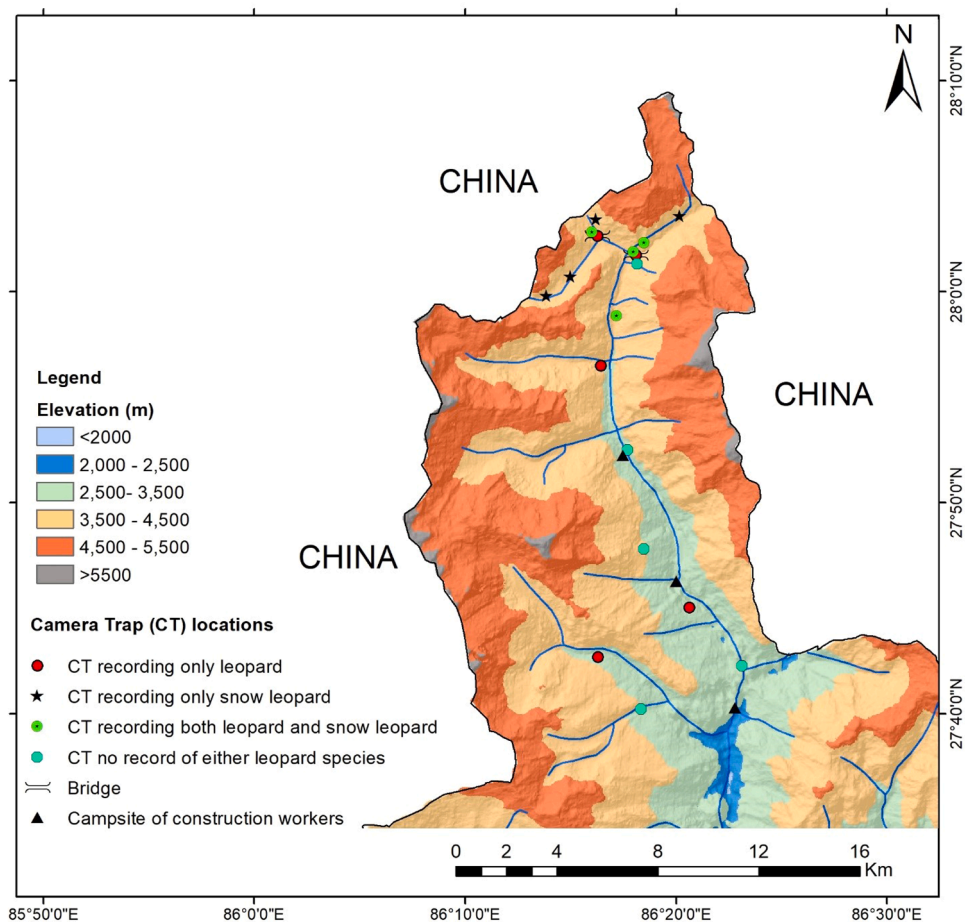


Fig. 1. Map showing the Lapchi Valley in the Gurishankar Conservation Area, locations where camera traps were placed, construction sites, and leopard species recorded in the study area.

as Eastern Tibet, Mount Gonggashan, Sichuan, and Sanjiangyuan Nature Reserve in Qinghai (Wen, 2016; Yang et al., 2021). In Baixueshan Nature Reserve in NW Yunnan, leopards were photographed at 3000–4500 m elevation where snow leopards were also reported to be present (Buzzard et al., 2017). In Nepal, snow leopards and leopards have been photographed at the same location in Annapurna-Manaslu (Chetri et al., 2019), and the Gaurishankar Conservation Area (GCA) (Chetri et al., 2023; Koju 2023a). A study in Sagarmatha reported that these two leopard species have similar diets but utilized different habitats (Lovari et al., 2013a). However, there is limited information regarding diet and activity overlap between leopards and snow leopards in other study areas (Lovari et al., 2024).

During a seven-month period between 2018 and 2019, Koju et al. (2021a) recorded the first photographic evidence (via camera traps) of a snow leopard in Lapchi Valley, GCA at an elevation above 3500 masl. However, there was no photographic evidence of leopards in the snow leopard's habitat at that time. Recent studies by Chetri et al. (2023), Koju (2023a), and Koju et al. (2023) have documented the presence of both leopards and snow leopards in the same habitat in the Rolwaling area and Lapchi Valley of Gaurishankar Conservation Area.

The present study addresses the potential for interspecific competition between these two vulnerable big cat species in Lapchi Valley. We hypothesize that the appearance of leopards in higher elevations is a sign of changing ecological dynamics, with significant implications for the conservation of snow leopards. This study aims to document the habitat and temporal overlap of leopards and snow leopards and to address the possible implications of competitive interactions in the Lapchi Valley, a region of critical transboundary significance between Nepal and China.

2. Methods

2.1. Study area

Lapchi Valley is situated within the Gaurishankar Conservation Area (GCA), a location renowned for its exceptional climatic diversity. Located between 86°10'32.53"E to 86°29'9.45"E and 28°20'13.19"N to 28°21'54.55"N. Lapchi Valley covers an area of approximately 290 sq. km with an elevation range from 968 to 7181 m above sea level (masl). The area encompasses a range of bioclimatic zones from sub-tropical to nival, offering a diverse array of habitats. It features 16 major vegetation types, 565 floral species, and a rich faunal diversity, including 235 bird species, 77 mammal species, 16 fish species, 22 reptilian species, and 10 amphibian species. The GCA holds particular significance for snow leopards and other wildlife because it links several habitats including the Tibetan Plateau to the north, Langtang National Park to the west, and Sagarmatha National Park to the east (Fig. 1). The area experiences major precipitation in the form of rain during the summer monsoon from June to August, and snowfall from January to March (Awasthi and Singh, 2015; Koju et al., 2020, 2021b; Pandey et al., 2021; Chetri et al., 2022).

In the past, Lapchi Valley has not been connected to networks of transportation and communication, but this is rapidly changing with recent hydropower projects and road construction (Fig. S1). It has traditionally been considered one of the holiest sites for Buddhists due to its isolation and the beliefs of the local people who follow the 'Beyul' culture. This is a culture of respect for the lives of animals and the ideologies that uphold taboos against actions and behaviors that destroy the environment. Beyul sites are "closed" by religious rituals to preserve them (Skog, 2010; Koju et al., 2020, 2021a), and thus, hunting and resource extraction is prohibited. The unique religious significance of this area motivates the local community to actively pursue a harmonious coexistence with the diverse wildlife, notably the snow leopards. Despite these conscientious efforts, the pastoralists in Lapchi Valley frequently deal with the challenges posed by the predation of their livestock by both snow leopards and Himalayan black bears (Koju et al., 2021a).

2.2. Camera Trap (CT) surveys

Our study was designed to systematically investigate the distribution and activity rhythms of elusive carnivores, notably leopards and snow leopards, across a mountainous region varying in elevation from 2200 masl to 4700 masl. To achieve this, we conducted camera trap (CT) surveys over a total of 25 months in two phases: i) from 22 October 2018–16 May 2019, and ii) from 19 October 2021–15 March 2023. The study area was stratified into a grid of 18 squares, each with an area of 2 km × 2 km. We employed a stratified random sampling method to select 16 squares from the grid, ensuring an unbiased representation of the various habitats within the study area. Given the logistical and financial constraints inherent in conducting extensive field research in remote, mountainous areas, we deployed a practical yet scientifically sound number of 16 camera traps across the designated grid squares. We targeted specific locations within these squares based on topographical features, vegetation cover, and the presence of scats, scrapes, and signs of prey species. We also follow the best practices for maximizing carnivore detections on trails, as documented by (Koju et al., 2023), while also considering potential prey pathways (Suryawanshi et al., 2021). Two additional camera traps were placed on the bridges that connect two different habitats only during the winter season to record any wildlife that might use the bridges. One bridge was very narrow, made from a wooden tree trunk less than 50 cm wide and the other was a plank bridge nearly 1.2 m wide. These bridges are used by local people, yak, horses, and dogs for crossing the river. The lowest CT location was at an elevation of 2247 masl and the highest was at 4628 masl. All CTs were set in hybrid mode to take both photographs and videos simultaneously. During the study, we experienced the loss of eight camera traps due to malfunction/theft. To ensure continuity and consistency in data collection, we adhered to a standardized protocol for promptly replacing lost and malfunctioning cameras at their original locations. This response enabled us to maintain a consistent data collection process, although it is acknowledged that the resulting datasets from these particular locations were incomplete. The focus of our study on the activity rhythms of carnivores provided a robust framework for analysis that is less susceptible to the variations that might arise from a reduced number of functional camera traps. All the camera

locations were a minimum of 2 km from each other except four camera traps that were located on either side of the river between the forest habitat and the alpine area of Lapchi Valley. Camera traps were strategically positioned at a height ranging from 30 to 40 cm above ground, considering the terrain's slope (Wangdi et al., 2019; Koju et al., 2020). The sampling design of our study has limitations regarding the accurate capture of prey species movement and activity. This is primarily due to the reliance on predator trails for camera trap placement, which may not coincide with the typical movement patterns of prey species. As a result, the recorded presence of prey species may be limited to the areas covered by the installed camera traps.

To prevent undesired image captures caused by direct sunlight, the camera sensors were oriented away from the sun, aligning with the established procedure outlined by Rovero et al. (2010). A standardized one-second trigger time was implemented between activation events. Operating continuously for 24 hours daily, the cameras utilized infrared Light Emitting Diodes (LEDs) to capture nocturnal images. Data from CTs were used for relative abundance index, activity pattern, and predator response. To maintain data integrity and ensure camera functionality, the CTs were visited eight times throughout the study period to perform data retrieval and battery replacement.

2.3. Relative Abundance Index

For the analysis of camera trap data, distinct images featuring individuals of the same species, with intervals of 30 minutes or more between captures were treated as separate events. Successive photographs featuring different individuals, whether of the same or different species, as well as non-consecutive images of individuals of the same species at a given site, were considered independent (Carbone et al., 2001). Images that were blank or where the species could not be identified were excluded from the analysis. The index of abundance of mammals recorded by CTs was calculated as a Relative Abundance Index (RAI) = $A/N \times 100$ where A is the total number of detection events of a species by all cameras and N is the total number of camera trap days by all the cameras throughout the study area (Jenks et al., 2011; Debata and Swain, 2018).

2.4. Activity patterns and temporal overlap

The photographs and videos captured during the study period were used to assess activity patterns and temporal overlap. The "Overlap" package (Meredith and Ridout, 2014) in R software was used for analysis.

Temporal overlap is defined as the area under the curve formed by the minimum of two kernel densities estimated at each time point for a pair of species (Ridout and Linkie, 2009). The R "overlap" package was used to perform the analysis and estimate temporal overlap for species. Species with less than four detections were not used in the analysis (Meredith and Ridout, 2014). The coefficient of overlap, Δ , ranges from 0 (no overlap) to 1 (complete overlap) and is categorized as very strong overlap if $\Delta > 0.80$, strong $0.60 > \Delta \geq 0.80$, moderate if $0.40 > \Delta \geq 0.60$, low if $0.20 > \Delta \geq 0.40$, and very low if $\Delta \leq 0.2$, in a partial modification of Mosquera-Muñoz et al. (2014). The coefficient of overlap Δ was estimated with 1000 bootstrap samples with a 95% confidence interval (CI) following Ridout and Linkie (2009) and Meredith and Ridout (2014).

The temporal overlap analysis was carried out in two categories: 1) Overlap between snow leopard and leopard and of each with their prey from the CTs where they shared habitat and 2) temporal overlap of snow leopards with prey before leopards were recorded in that habitat. The temporal behavior pattern of snow leopards after the arrival of the leopard also was assessed and analyzed in overlap pattern, similarly, the temporal behavior patterns of snow leopards and leopards were analyzed from the CTs where one of the leopard species was not recorded. Based on the diet composition described in Koju et al. (2023) prey were identified and categorized into wild prey and livestock. The list of prey species is similar to that mentioned by Lovari et al. (2013a) from Sagarmatha National Park, a protected area adjoining our study area. However, it is important to note that blue sheep are not present in Sagarmatha National Park. Actual predation rates may vary depending on the specific predator-prey dynamics and other local ecological factors.

The comparison of daily activity patterns and analysis of seasonal associations between leopards and snow leopards were conducted using Pearson's Chi-squared test. The recorded events were categorized into distinct time intervals: dawn (05:00 – 07:00), day (07:00–17:00), dusk (17:00 – 19:00), and night (19:00–05:00). This classification aligns with established protocols (Noor et al., 2017) and included partial modification to be consistent with average daylight records of Lapchi Valley. To ensure strength, the seasonal data analysis focused only on a single year (March 2022 to February 2023), acknowledging the integral variability in seasonal durations, particularly the uneven periods of summer and winter within the total dataset.

We analyzed seasonal effects by dividing the study period into two major seasons following Koju et al. (2023); whereby the warm and cold seasons were demarcated based on the local people's movement to seasonal pasture. The cold season was designated from 16 November to 15 April, when local herders with their livestock migrated to lower elevations from Lapchi Valley due to the cold and snow. The warm season was designated from 16 April to 15 November, when the people of Lapchi both herd on high pasture land with their livestock and plant barley and potatoes in the lower valley (Koju et al., 2023).

2.5. Response to the season and prey

The Generalized Linear Mixed Effect Model (GLMM) was employed for analysis with binomial outcomes, fitted by maximum likelihood (Laplace Approximation) to examine the factors influencing the presence of leopards and snow leopards. In this analysis, camera traps were treated as a random factor, while prey type and seasons were considered fixed factors. The dataset was divided based on leopard and snow leopard, and a binary coding system (0 for absence, 1 for presence) was applied for each entry, representing the presence or absence of either species of leopard with respect to camera traps, seasons, and prey types. The presence or absence

status of the leopards was determined by considering a season as "present" if at least one camera captured a photo of either species of leopard during that season. If no photos were captured for a particular camera trap throughout the entire season, it was labeled as "absent" for that specific camera trap. Model validation was performed using residual plots (i.e., examine residuals against predicted values) and Quantile-Quantile (Q-Q) Plot, and the saturation curves were checked before conducting the analysis to make sure there was stabilization of the activity pattern. We also employed a Pearson's Chi-squared test to investigate the potential association between the two leopard species and season in our study. To perform the GLMM, the glmer function was used under the lme4 package in R version 4.2.1 (R Core Team 2022).

3. Results

In total, we analyzed 1938 camera trap events of a variety of mammals and identified 39 independent sightings of snow leopards and 54 independent sightings of leopards. In addition to the snow leopards and leopards, 18 other species of wild mammals and two species of livestock were recorded by the camera traps (Table 1). Among the wild mammals, there was one Endangered species, four Vulnerable species, and four species with Near Threatened status per their listing in the IUCN Red List (accessed on December 12, 2023). Five of the species were listed as protected mammals by the Department of National Parks and Wildlife Conservation (DNPWC) Act of Nepal.

The RAI calculation showed the highest abundance was of Himalayan musk deer (13.83) followed by domestic yak and red fox, and the least was for the Himalayan marmot (0.26) followed by Asiatic golden cat (0.08), Siberian weasel (0.6), and Asian Palm Civet (0.06). The RAI for snow leopards was 2.61 and 3.62 for leopards (Table 1).

3.1. Spatio-temporal overlap

During our study, the first photograph of a leopard in an alpine area of Lapchi Valley was recorded on 15 June 2022 (4:07:39 AM) by Camera 9 (28.117027 N, 86.17486 E, elevation 3862 masl) close to the main monastery (Lapchi Gumba). Yak herders, local people, and monks confirmed that they never saw leopard in this habitat before our camera trap documentation. In this study, a total of eight CTs recorded snow leopards, and nine CTs (including the two on the bridges) recorded leopards. Five CTs did not record either leopard species and four CTs recorded both leopards and snow leopards between 15 June 2022, to 15 March 2023 (Fig. 1, Fig. 2, and Fig. 6).

A total of 29 events of leopards (53.70%) and 15 events of snow leopards (38.46%) were recorded in the area of habitat overlap. Snow leopard activity was recorded more often in non-overlapping areas than in overlapping areas, whereas leopards were recorded more in overlapping areas. Both snow leopards (89.74%), and leopards (62.96%) were recorded with higher frequency in the cold season than in the warm season. Further, a chi-square test indicated that the daily activity pattern of snow leopards changed

Table 1

List of mammals recorded from October 2018 to March 2023 by camera traps in the Lapchi Valley.

Mammal record	Scientific name	IUCN Red list	CITES	Events	CT days	No. of Recorded CT locations	Elevation (masl)		RAI
							Lowest	Highest	
1.Asian palm civet	<i>Paradoxurus hermaphroditus</i>	LC		1	84	1	2247	2247	0.06
2.Asiatic golden cat	<i>Catopuma temminckii</i>	NT	II	4	84	1	2247	2247	0.26
3.Assamese macaque*	<i>Macaca assamensis</i>	NT	II	25	1040	4	2247	3555	1.67
4.Beech marten	<i>Marted foina</i>	LC	-	17	394	2	3843	3860	1.14
5.Blue sheep	<i>Pseudois nayaur</i>	LC	III	15	883	4	3860	4127	1
6.leopard	<i>Panthera pardus</i>	VU	I	54	1989	9	2883	4058	3.62
7.Domestic yak	<i>Bos grunniens</i>			169	2535	10	2883	4127	11.34
8.Himalayan black bear	<i>Ursus thibetanus</i>	VU	I	29	1271	5	2883	3843	1.94
9.Himalayan goral	<i>Naemorhedus goral</i>	NT	I	15	333	1	2247	2247	1
Himalayan marmot	<i>Marmota himalayana</i>	LC	III	4	263	1	4103	4103	0.26
10.Himalayan musk deer*	<i>Moschus leucogaster</i>	EN	I	623	3165	13	3395	4127	41.81
11.Himalayan serow	<i>Capricornis sumatraensis</i>	VU	I	46	1442	7	2247	3593	3.08
12.Himalayan tahr	<i>Hemitragus jemlahicus</i>	NT	-	86	635	4	2247	3403	5.77
13.Himalayan wolf*	<i>Canis lupus</i>	LC	I	46	1272	5	3843	4628	3.08
14.Horse	<i>Equus caballus</i>			44	1621	5	2883	4127	2.95
15.Leopard cat*	<i>Prionailurus bengalensis</i>	LC	I	60	2015	9	2883	4127	4.02
16.Rattus sp.	<i>Rattus sp.</i>			15	272	2	2247	3593	1
17.Red fox	<i>Vulpes vulpes</i>	LC	III	112	2690	11	3395	4127	7.51
18.Royle's pika	<i>Ochotona roylei</i>	LC	-	26	570	3	3205	4058	1.74
19.Siberian weasel	<i>Mustela sibirica</i>	LC	III	9	901	3	2883	4127	0.6
20.Snow leopard*	<i>Panthera uncia</i>	VU	I	39	2063	8	3535	4628	2.61
21.Yellow-throated marten	<i>Martes flavigula</i>	LC	III	51	1930	7	2883	4058	3.42

Note: * Protected mammals of Nepal

RAI = Relative Abundance Index

CITES = Convention on International Trade in Endangered Species of Wild Fauna and Flora



Fig. 2. Camera Trap (CT) recordings of snow leopards (photos '1' and leopards (photos '2') coexisting in a shared habitat were captured at varying elevations: A) 3901 masl, B) 4048 masl, C) 3843 masl; and D) 3535 masl. Note: Fig. D2 is a screenshot from the video recorded by CT (video is available in a supplementary file).

significantly by season (Chi-square = 15.114, df = 1, p-value = 0.000101), but activities of the leopards were not affected by season (Chi-square = 3.1887, df = 1, p-value = 0.07415).

The highest elevation of recorded overlap was at 4058 masl in an alpine habitat (Fig. 2[B]) on a human-maintained trail to the 'kharka' (pasture land). The lowest elevation of recorded overlap was at 3535 masl (Fig. 2[D]) in an *Abies* and *Juniper* forest near the river and very close to the alpine habitat. Leopards were recorded (n=5) crossing the bridges over both rivers at an elevation of 3700 masl, crossing from the forest habitat in the south to the alpine area in the north and vice versa (Fig. 3).

The Overlap coefficient (Δ) between snow leopards and leopards was strong in the area where the snow leopards and leopards were recorded together ($\Delta=74$, Fig. 4 [A1]). The temporal activity pattern of snow leopards in Lapchi Valley before the arrival of leopards was significantly different (Pearson's Chi-squared test with Yates' continuity correction = 8.7754, df = 3, p-value = 0.03). The snow leopards' activity was concentrated during early sunrise and after sunset to midnight before 15 June 2022 (when leopards were first recorded in that area). Following the arrival of leopards in the study area, the snow leopards' activity appeared to shift from early mornings before and after sunrise to times before and after sunset (Fig. 4 [A2]).

The Overlap coefficient ($\Delta=0.44$) regarding the activity of the snow leopards before and after the arrival of leopards is only moderate. Furthermore, the activity pattern of snow leopards in the areas where only they were recorded (absence of leopards) suggested they were strongly nocturnal (Fig. 4 [A3]). Regarding the activity of leopards in the areas where only they were recorded (no record of snow leopards), the results showed that leopards were active throughout all periods of time, but showed the least activity at mid-day. (Fig. 4 [A4]).

Similarly, the temporal overlap coefficient (Δ) between snow leopards with wild prey and livestock showed that snow leopards had a strong overlap with wild prey species in habitats shared with leopards (0.70 [0.57–0.92]) but only moderate overlap in habitats without leopards (0.56 [0.39–0.75]). The overlap of leopards with wild prey was recorded as strong in habitats shared with snow leopards (0.69 [0.56–0.79]) and in habitats without snow leopards (0.67 [0.51–0.94]). Snow leopards had moderate overlap with livestock in the pooled data ($\Delta=0.46$ [0.33–0.57]) and in the presence of leopards (0.44 [0.26–0.6]) but low overlap when leopards were absent (0.38 [0.18–0.54]). Leopards showed low overlap with livestock in both the presence ($\Delta=0.28$ [0.11–0.34]) and absence ($\Delta=0.39$ [0.22–0.69]) of snow leopards (see Table 2 and Fig. 4, Fig. 5, Fig. 6, and Fig. 7).

3.2. Presence of leopards and snow leopards in response to season and prey type

The study revealed a significant relationship between seasons and prey type in the presence of snow leopards, with substantial



Fig. 3. Leopards using the two bridges over the rivers in Lapchi Valley to cross from forest habitat to alpine habitat (above tree line) at an elevation of 3700 masl.

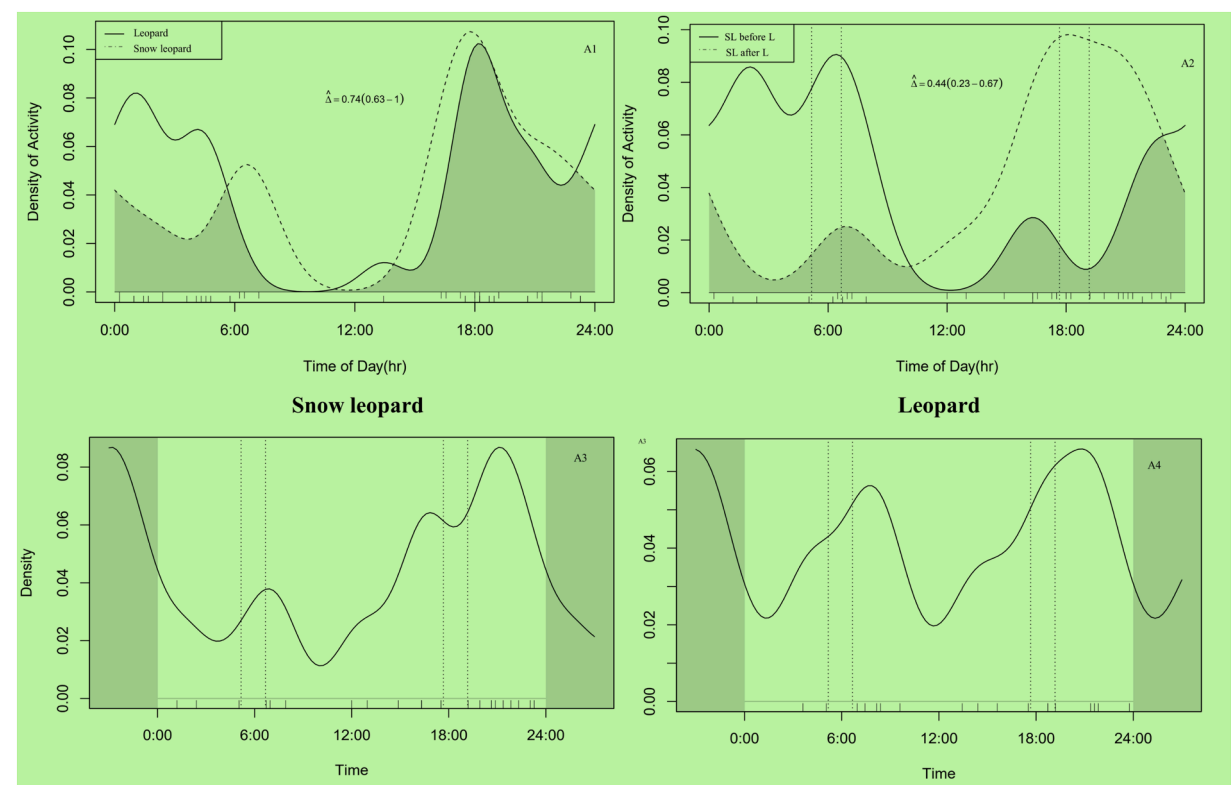


Fig. 4. A1) Temporal co-occurrence of snow leopards and leopards in the study area based on data from CTs where both leopard species were recorded (N=8); A2) Activity pattern of snow leopards before and after the appearance of leopards in snow leopard habitat; A3) Activity pattern of snow leopards in the regions exclusively inhabited by snow leopards; A4) Activity pattern of leopards in regions exclusively inhabited by leopards.

Table 2

Overlap of snow leopards and leopards with their prey under three conditions: both leopard species recorded; only snow leopard recorded; and only leopards recorded.

SN	Conditions	CT days	Events (N)	Group 1	Group 2	Overlap coefficient (Δ) with (CI)	Overlapping degree
1.	Using data where both leopards were recorded	1334 (CT no=4)	801	SL	L	0.74 (0.63–1.0)	Strong
				SL	Wild prey	0.70 (0.57–0.92)	Strong
				SL	Livestock	0.44 (0.26–0.6)	Moderate
				L	Wild prey	0.69 (0.56–0.79)	Strong
				L	Livestock	0.28 (0.11–0.34)	Low
2.	Only snow leopards were recorded	759 (CT no=4)	195	SL	Wild prey	0.56 (0.39–0.75)	Moderate
				SL	Livestock	0.38 (0.18–0.54)	Low
3.	Only leopards were recorded	655 (CT no=6)	343	L	Wild prey	0.67 (0.51–0.94)	Strong
				L	Livestock	0.39 (0.22–0.69)	Low

Note: SL= snow leopard, L= leopard

variability observed among camera traps. The log odds of snow leopards in the GLMM analysis being present were higher during the cold season compared to the warm season, a pattern that was not observed for leopards. Species increased significantly in the presence of wild prey compared to livestock (Table 3).

The models considered the warm season and livestock (prey types) as reference categories.

4. Discussion

4.1. Competition and coexistence

The findings of this study highlight the significance of interspecific competition in wildlife ecology, particularly in the context of shifting habitats of two leopard species. The significant habitat and temporal overlap documented between snow leopards and leopards in Lapchi suggest that interspecific competition may be a consequence of environmental shifts and human activity. Our findings are

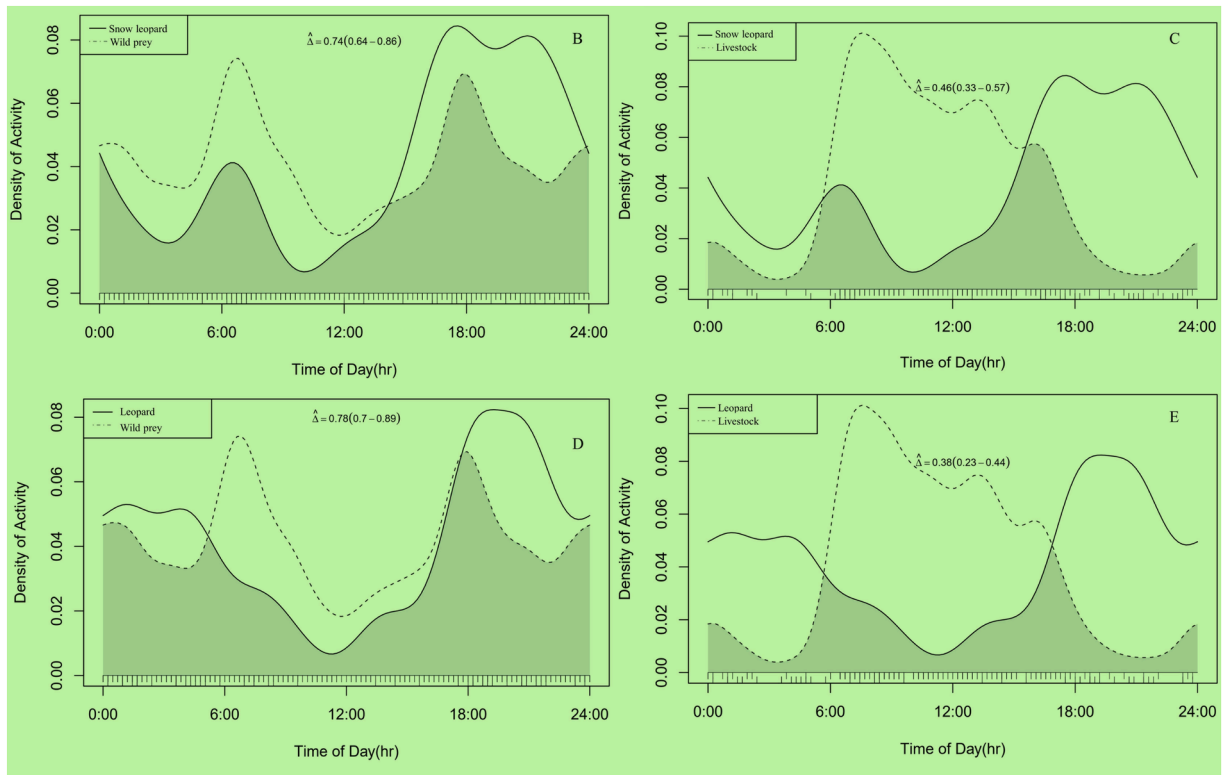


Fig. 5. Co-occurrence of snow leopards, leopards, and their prey across all camera trap locations: B) Snow leopards and wild prey; C) Snow leopards and livestock; D) Leopards and wild prey; and E) Leopards and livestock.

similar to the overlap and potential competition found by Pal et al. (2022) in the western Himalaya although they found overlap only in winter when snow leopards come down to lower elevations. We found significantly more records of snow leopards in winter, and future work may require more cameras placed at higher elevations to assess the potential upward movements of snow leopards in summer. Our results differed from Lovari et al. (2013a) in nearby Sagarmatha National Park where both leopard species had similar diets but utilized different habitats. In Lapchi, both leopards and snow leopards shared the same habitat but further study is needed to address the degree of diet overlap. In Lapchi, Koju et al. (2023) conducted a micro-histological analysis on 20 purported snow leopard scats collected above 3800 masl and found that blue sheep (*Pseudois nayaur*) were the most common wild prey item in the scats while horses were the most common livestock prey. In Sagarmatha, blue sheep are absent and this likely affects predator-prey dynamics for the leopard species in that area.

4.2. Spatio-temporal overlap

Our results suggest that the presence of leopards may have affected the activity patterns of snow leopards. In the presence of leopards, the snow leopard's activity patterns appeared to shift from pre-dawn to late afternoon and evening (Fig. 4 [A2]) with only moderate overlap in activity pattern ($\Delta=0.44$). The temporal overlap of snow leopards with wild prey and livestock in habitats where only snow leopards were present showed that they had moderate overlap with wild prey ($\Delta=0.56$) and less overlap with livestock ($\Delta=0.38$). Meanwhile, when leopards were present, snow leopards had strong overlap with wild prey ($\Delta=0.70$) and moderate overlap with livestock ($\Delta=0.44$). While these differences are not large, they appear to indicate that snow leopards were affected by the presence of leopards, with a shift to more diurnal activity and more overlap with wildlife and livestock. In contrast, in the presence of snow leopards, leopards did not show any change in overlap with wild prey and had less overlap with livestock, a shift from $\Delta=0.39$ to $\Delta=0.28$ (See Fig. 7 and Table 2).

In our study, both species of leopards were photographed more during the winter season, a period characterized by reduced human activity in the study area when herders move their livestock to lower elevations. This observation supports the notion that human interference is a significant factor influencing the movement of wildlife (Taylor-Brown et al., 2019; Koju et al., 2021c; Lewis et al., 2021). Gaynor et al. (2018) and Doherty et al. (2021) have similarly demonstrated a pronounced impact of human presence on the daily activity patterns of wildlife, surpassing landforms, habitats, and taxa. More photographs of snow leopards may reflect the use of lower elevations in winter as found by Pal et al. (2022).

Lovari et al. (2013a) studied snow leopards and leopards at Sagarmatha National Park, which borders GCA. They found that both leopard species prey upon similar wild and domestic species, with dietary overlap recorded at 69% annually (76% during the winter

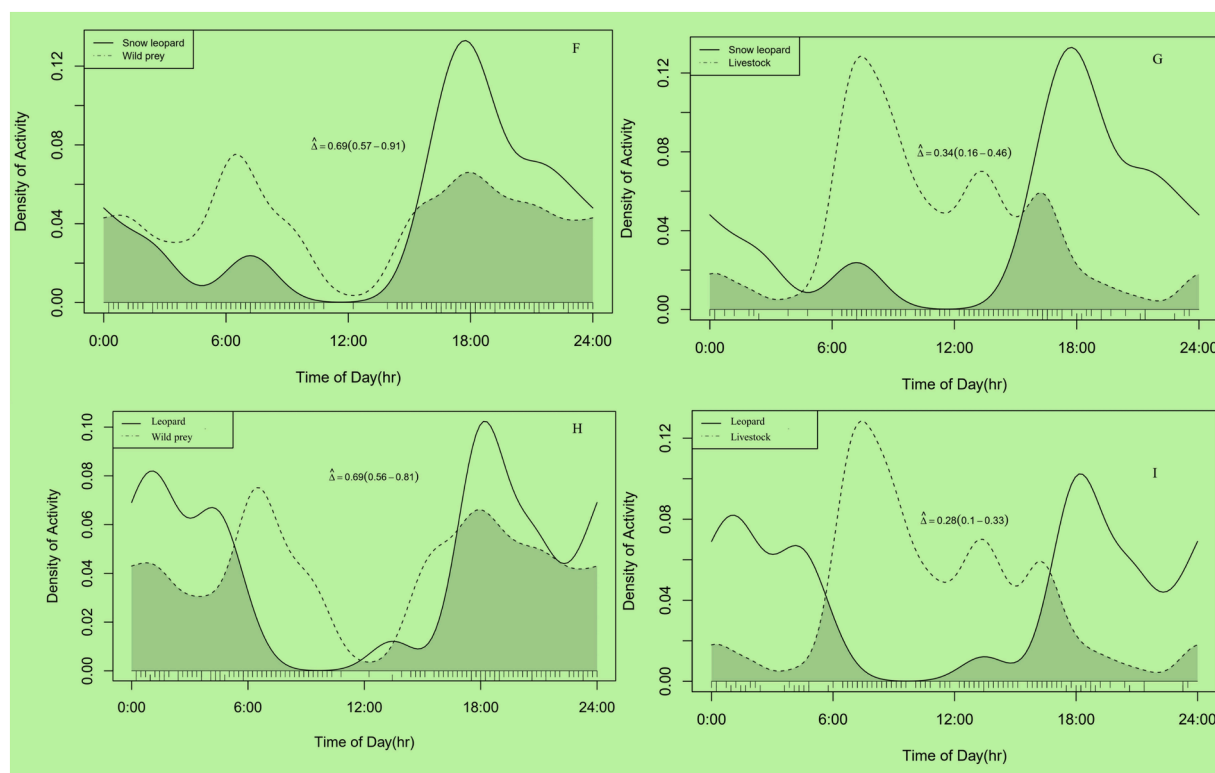


Fig. 6. Co-occurrence of snow leopards, leopards, and prey across four camera trap locations where both leopard species were recorded: F) Snow leopards and wild prey; G) Snow leopards and livestock; H) Leopards and wild prey; I) Leopards and livestock.

months, and 60% during the summer months) but had only limited spatial overlap. In our study, however, there was substantial habitat overlap. This supports the potential for escalating pressure on prey species and heightened competition among predators. The different distribution patterns may also reflect differences in the spatial availability of local prey as Sagarmatha National Park versus Lapchi Valley. As noted earlier, Sagarmatha National Park does not have blue sheep, whereas they are common in Lapchi and were commonly found in the snow leopard scats (Koju et al., 2023).

The observed change in the activity pattern of snow leopards from morning to evening, coupled with the substantial overlap between the two leopard species in this study, suggests the initial stages of exclusion and the avoidance of encounters. This dynamic may eventually lead to the local displacement of one of the leopard species, potentially favoring the leopard due to its dominance in size as well as its ability to utilize more habitats compared with snow leopards (Lovari et al., 2013a). These differences may be due to the effects of the leopards on the potential prey of the snow leopards, or there might be age/sex differences in both species. The noteworthy observation of leopards using the bridges in Lapchi Valley to navigate rivers and move from forest habitats to alpine regions further supports the notion that leopards exhibit greater adaptive behavior thus giving them a competitive edge over snow leopards.

4.3. Conservation challenges: linear infrastructure and anthropogenic activities

The development of roads may exert pressure on the movement and activity of predators (Sharief et al., 2022). Further, infrastructure development projects in the area have also likely impacted the ranging of both leopard species, especially leopards that occur in the same elevations as the construction to date. Records of leopards at lower elevations were rare in comparison to alpine habitats thus supporting the likelihood of construction having an impact on their movement. A road in the study area that is still under construction now connects Lapchi and Lamabagar in anticipation of two major hydropower dams scheduled for construction in Thangjemo and Yuluk. Since 2020, three locations along the road's route (Deurali Lamabagar: 27.953638 N, 86.216035 E elevation 2208 masl, Yuluk: 27.99871305 N, 86.19191805 E, elevation 2433 masl, and Thangjemo 28.04365650 N, 86.17013101 elevation 3177 masl) have accommodated worker camps with 15–30 workers operating heavy equipment such as bulldozers, pressure pumps, excavators, and generators. The construction work involves activities such as blasting, road widening, and tree cutting that lasts 12–16 hours a day. This incessant activity may have compelled the leopards and their prey to relocate from lower elevations to the less disturbed alpine areas of the valley.

The Lapchi residents primarily engage in animal husbandry, adopting a semi-nomadic lifestyle focused on raising yaks and horses. Traditionally, they trade these livestock with neighboring villages in Tibet, China, a journey spanning one day on foot (Koju 2023b).

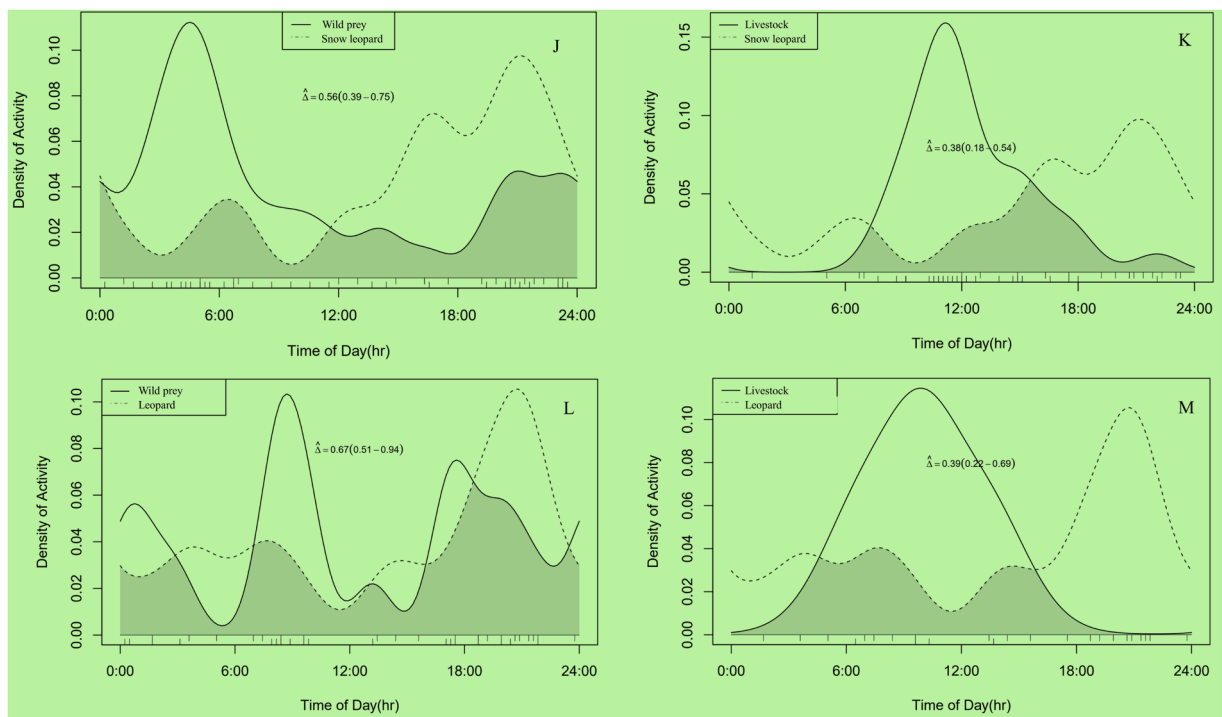


Fig. 7. Co-occurrence of snow leopards with different prey types: J) wild prey, and K) livestock across four camera trap locations where only snow leopards were recorded; Co-occurrence of leopards with different prey types: L) wild prey, and M) livestock across four camera traps locations where only leopards were recorded.

Table 3

Results of the GLMM.

Species	β	SE	z-value	p-value
Snow leopard				
Season (cold vs warm season)	29.006	5.595	5.184	< 0.001 ***
Prey type (livestock vs wild prey)	5.473	1.950	2.807	< 0.005 **
Leopard				
Season (cold vs warm season)	-0.354	0.865	-0.409	> 0.05
Prey type (livestock vs wild prey)	1.986	0.379	5.246	< 0.001 ***

Note: SE: Standard error,

However, the COVID-19 lockdown resulted in the closure of borders, halting this essential trade. Consequently, local residents have been unable to sell their livestock since March 2020, leading to an increasing population of horses and yaks in the pastures of Lapchi Valley (Koju 2023a). Changing abiotic and biotic conditions, such as livestock grazing and limited prey resources, affect the coexistence and spatial interactions between snow leopards and leopards (Pal et al., 2022), and this surge in livestock abundance in Lapchi may have contributed to an increase in leopard activity as well. Miller et al. (2016) affirmed that the increased abundance of livestock can intensify the movement of predators and escalate instances of depredation. The scenario in Lapchi Valley, with an elevated concentration of livestock due to trade restrictions, potentially serves as a parallel, drawing leopards to higher elevations in search of ample prey resources.

In the Lapchi Valley's pasture area, there were no documented instances of human-wildlife conflict from livestock depredation by predators such as the leopard, wolf, or snow leopard, until 2019. The only instances of conflict were occasional Himalayan black bear attacks on humans (Koju et al., 2020, 2021a). However, a notable shift occurred in 2022, marked by the reported loss of at least seven horses and three yak calves (Koju et al., 2023). The amount of livestock depredation has increased (as per communication with local herders) since 2020. Local people are also experiencing the loss of larger-sized yaks and horses than in previous years. Further, the larger prey are easier targets for leopards compared to the snow leopards. This suggests an emerging trend of heightened competitive interactions among carnivores, likely tied to increased diet overlap, as found by Donadio and Buskirk (2006).

4.4. Climate change and changing ecosystems

As a result of ongoing climate change, the warmer and wetter conditions in the Himalayas also may be resulting in forest expansion and forest wildlife shift (like leopards), into higher alpine areas, the snow leopards' preferred habitat. There is a limit to how high snow leopards can ascend as they will face a shortage of prey at higher altitudes. According to a study conducted by WWF, impacts from climate change could result in a loss of up to 30 percent of the snow leopard habitat in the Himalayas (Forrest et al., 2012; WWF, 2012). The increasing grassland and forest cover in Lapchi Valley (ICIMOD, 2022) may be a factor driving leopards to higher elevations. Climate change has caused upward shifts in the tree line and vegetation, resulting in habitat shrinkage and fragmentation for snow leopards as noted in other studies (Kazmi et al., 2021; Pal et al., 2022).

. The increase in infrastructure development in Lapchi also may have influenced leopard distribution. Khan et al. (2021) showed that land use and land cover change have a significant impact on the distribution of snow leopards in Pakistan.

4.5. Implication for conservation

The co-occurrence of snow leopards and leopards in Lapchi Valley holds pivotal implications for biodiversity conservation. This ecological phenomenon signals the Lapchi Valley's role as a biodiversity hotspot, connecting Sagarmatha and Langtang National Parks in Nepal to the Qomolangma National Nature Preserve on the Tibetan plateau. The presence of both leopard species signifies a strong and interconnected ecosystem, emphasizing the area's ecological richness. The documented spatial and temporal overlap between the two leopard species emphasizes the necessity for comprehensive conservation strategies, addressing potential resource competition and conflicts (Lovari et al., 2024). Moreover, the transboundary nature of Lapchi Valley requires collaborative initiatives between Nepal and China for effective conservation management, highlighting the broader significance of this discovery for the preservation of these apex predators and their habitats across international borders.

The implications of our study are twofold. Firstly, they highlight the need for proactive and adaptive management strategies that consider the dynamic nature of predator-prey relationships in a changing climate with anthropogenic activities. Conservation efforts should focus on maintaining the integrity of snow leopard habitats and ensuring the availability of wild prey to minimize the potential for livestock depredation. Secondly, the documented habitat overlap underscores the importance of transboundary conservation initiatives. The ecological continuity across borders necessitates collaborative management efforts between Nepal and China to effectively preserve these species. This need for transboundary management is highlighted by the snow leopard scats that contained domestic goat (*Capra hircus*), a livestock species that is not raised in the Lapchi Valley and is strong evidence for cross-boundary ranging (Koju et al., 2023).

The study also opens up several avenues for future research. First, diet analyses with genetic confirmation of scats could provide insight into the degree to which the leopard species overlap in diet and might help us learn more about the different snow leopard and leopard habitat overlap at Lapchi and nearby Sagarmatha, where there are no blue sheep. A better understanding of leopard diets would also help us learn more about livestock depredation and how to mitigate conflict with local herders. Longitudinal monitoring of the two leopard populations could provide deeper insights into the long-term impacts of habitat overlap. Additionally, investigating the behavioral ecology of these predators in response to climate change and human expansion could inform conservationists about potential stressors and adaptive strategies employed by these species, especially the long-term impact of infrastructure development and potential ecotourism in the Lapchi Valley.

5. Conclusion

Our study demonstrates significant spatial and temporal overlap between snow leopards and leopards. The presence of both species was strongly linked to the availability of wild prey, emphasizing the pivotal role of prey dynamics in shaping leopard presence. Furthermore, anthropogenic activities are reshaping wildlife habitats and behaviors adding urgency to conservation efforts. Strategies must address interspecific competition and changing habitat conditions. Conservation measures should prioritize habitat conservation management of human-wildlife conflict and maintenance of prey populations. The findings also highlight the critical importance of international cooperation to ensure the long-term survival of these apex predators and the conservation of their ecosystems.

CRediT authorship contribution statement

Narayan Prasad Koju: Conceptualization, Methodology, Field work, Investigation, Validation, Formal analysis, Writing original draft, Writing review & editing, Funding acquisition, Visualization. **Paul Buzzard:** Field work, Writing review & editing, Funding. **Arati Shrestha:** Formal analysis, Validation, Writing review & editing. **Shailendra Sharma:** Formal analysis, Validation, Writing review & editing. **Juan Li:** Validation, isualization Writing review & editing, **Kai He:** Validation, Visualization, Writing review & editing, **Randall C. Kyes:** Validation, Writing review & editing, Funding acquisition. **Cheng Chen:** Validation, Writing review & editing, Funding acquisition. **WVB:** Validation, Writing review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e02953](https://doi.org/10.1016/j.gecco.2024.e02953).

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