

Landscape predictors influencing livestock depredation by leopards in and around Annapurna Conservation Area, Nepal

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ABSTRACT

Livestock depredation by leopards is a pervasive issue across many Asian and African range countries, particularly in and around protected areas. Developing effective conflict mitigation strategies requires understanding the landscape features influencing livestock depredation. In this study, we investigated predictors associated with livestock depredation by leopards using 274 cases of leopard attacks on livestock that occurred between 2017 and 2020 in the Annapurna Conservation Area, Nepal. We also examined how livestock predation by leopards varied depending on the species, season, and time. A generalized linear model with binary logistic regression was used to test the statistical significance of variables associated with the presence and absence of conflict sites. The results revealed that the area of forest, agricultural land, length of rivers, slope, proximity to settlements and protected areas, and elevation significantly predicted the probability of leopard attacks on livestock. We also observed a significant increase in the incidence of leopard predation on livestock with decreasing slopes and rising elevations. The areas near human settlements and the protected areas faced a higher risk of leopard predation. The incidence of leopard predation on livestock varied significantly depending on the livestock species, season, and time. Goats were the most highly predated livestock, followed by sheep, cow/ox, and buffalo. A total of 289.11 km² (or around 5% of the research area) was deemed to be at high risk for leopard predation on livestock. This study's comprehensive understanding of human-leopard conflicts provides valuable insights for planning and implementing measures to reduce damage caused by leopard populations throughout their range.

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INTRODUCTION

Addressing the global challenge of human-wildlife conflict is an urgent issue faced by managers and policymakers (Sharma et al., 2020; Torres, Oliveira & Alves, 2018). This conflict arises from the shared use of resources by humans, livestock, and wild predators (Venumière-Lefebvre, Breck & Crooks, 2022; Shrestha et al., 2022; Graham, Beckerman & Thirgood, 2005; Treves & Karanth, 2003). In cases of human-large carnivore conflict, animals kill livestock (Dalerum, Selby & Pirk, 2020; Lamichhane et al., 2018) and occasionally pose a threat to humans (Inskip & Zimmermann, 2009; Woodroffe et al., 2007), leading to their persecution by people (Mateo-Tomás et al., 2012). Carnivore habitats are increasingly fragmented and resource-scarce due to human population growth, anthropogenic activity reduced wild prey, and changing land use, resulting in human-carnivore conflicts (Dheer et al., 2022; Naha et al., 2020; Acharya et al., 2017; Inskip & Zimmermann, 2009). For instance, rapid human population growth and habitat encroachment on common leopard (Panthera pardus, referred to as "leopard" hereafter) habitats have led to reduced prey availability and habitat fragmentation. Those pressures drive leopards to forage closer to human settlements, leading to frequent human-leopard conflicts (Puri et al., 2020; Yadav et al., 2020; Stein et al., 2016).

The leopard is categorized as Vulnerable by the International Union for Conservation of Nature and Natural Resources (IUCN) Red List (*Stein et al.*, 2016) and listed as Appendix 1 in CITES law. The National Red List of Mammals categorizes it as an endangered species. The legal status of this species in Nepal is Protected (Appendix 1) under the National Parks and Wildlife Conservation Act 1973 (*Jnawali et al.*, 2011). Its populations are declining throughout most of their range (*Jacobson et al.*, 2016; *Athreya et al.*, 2011), leading to isolation, with some Asian subspecies now assessed as endangered and critically endangered on the IUCN Red List. They are widely distributed across Africa and Asia, but their historical range has seen a significant 61% reduction (*Stein et al.*, 2016). The leopard is distributed in Nepal from the lowland Terai region to the mid-hill areas (*Baral et al.*, 2023; *Koirala et al.*, 2012), and recent observations indicate sightings at elevations of up to 4,500 meters in Annapurna Conservation Area (Bikram Shrestha, 2023, pers. comm.). However, their population status and occupancy are poorly understood (*Lamichhane et al.*, 2021).

Numerous studies have been conducted to examine the spatio-temporal patterns and frequency of leopard predation on livestock in Nepal (*Kandel et al.*, 2023; *Adhikari et al.*, 2022; *Dhungana et al.*, 2019; *Lamichhane et al.*, 2018; *Karki & Rawat*, 2014; *Koirala et al.*, 2012; *Sijapati et al.*, 2021). The Department of National Parks and Wildlife Conservation (*DNPWC*, 2017) reported that leopards were responsible for 78% of livestock kill incidents in Nepal. Furthermore, *Adhikari et al.* (2022) identified the mid-hills regions as the areas with the highest risk for leopard predation on livestock. Likewise, similar studies have

been conducted outside of Nepal (Akrim et al., 2021; Naha, Sathyakumar & Rawat, 2018; Shehzad et al., 2015; Constant, Bell & Hill, 2015; Qamar et al., 2010).

Few studies have been conducted on the influential factors affecting leopard predation on livestock (*Naha et al.*, 2020; *Yadav et al.*, 2020; *Rostro-García et al.*, 2016; *Constant, Bell & Hill, 2015*) and mapping conflict hotspots (*Yadav et al.*, 2020; *Sharma et al.*, 2020). However, all of these studies were conducted outside of Nepal. So far, studies that employ a robust sampling and modelling framework have not been conducted in Nepal. Identifying zones prone to leopard predation on livestock is crucial for efficient conflict mitigation and leopard conservation. Focusing resources and efforts on these areas allows for targeted livestock protection, reduces retaliatory killings of leopards, and engages communities in sustainable coexistence strategies (*Miller, 2015*). This approach addresses the complex challenges of human-leopard conflicts while safeguarding both local livelihoods and leopard populations (*Adhikari et al., 2022*; *Yadav et al., 2020*; *Mateo-Tomás et al., 2012*). Reckoning this fact, we have chosen the Gandaki Province of Nepal as our research site for these unexplored studies, particularly as it overlaps with the Annapurna Conservation Area. This region, situated in the mid-hills of Nepal, is a notable focal point for human-leopard conflict (*Adhikari et al., 2022*; *Koirala et al., 2012*).

To address the aforementioned research gaps, we aim to determine important landscape variables that can influence leopard predation on livestock by employing a binomial generalized linear model and map high-conflict-prone areas by utilizing significant environmental, anthropogenic, and topographic variables through MaxEnt modeling. In this study, we established hypotheses to investigate how different landscape factors influence leopard predation on livestock in Nepal. The study's primary objective was empirically assessing and confirming these hypotheses through data analysis and statistical methods. In addition, we conducted descriptive analyses to understand the spatio-temporal and predation patterns of leopards on livestock. The study's results are expected to enhance efforts to reduce human-leopard conflicts and promote coexistence between humans and leopards.

METHODOLOGY

Study area

The Annapurna Conservation Area (ACA), established in 1992, is Nepal's largest protected area, covering 7,629 sq. km. It is located in the hills and mountains of west-central Nepal (83057'E, 28050'N) and is managed by the National Trust for Nature Conservation (NTNC). The Annapurna Himalayas have various ecosystems, from subtropical woods to trans-Himalayan freezing deserts. The ACA is rich in biodiversity, home to 1,352 plant species, 128 wild mammal species, 514 bird species, 348 butterfly species, 40 reptile species, and 23 amphibian species (*NTNC National Trust for Nature Conservation, 2018*), and ranges in altitude from 790 m to the peak of Annapurna I at 8,091 m. It is the only protected area in Nepal where locals can live within the boundaries, own their private land, and keep their traditional rights and access to the usage of natural resources. The area is also a popular trekking destination for visitors from all over the world. To ease its management,

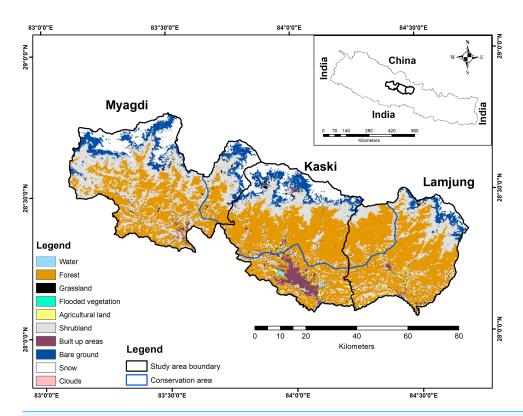


Figure 1 Study area boundary, showing the land cover and conservation area.

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ACA is divided into seven-unit conservation offices: Ghandruk, Lwang, Sikles, Bhujung, Manang, Jomsom and Lo-Manthang. The local community members reside in 15 rural municipalities of five districts and 87 wards. This study was conducted in three of the five Gandaki province districts (Kaski, Lamjhung, and Myagdi), which overlap with the ACA (Fig. 1). Myagdi and Lamjung districts cover relatively smaller parts of the conservation area (approximately 413.46 km² and 386.41 km²), and Kaski district covers the largest part of the conservation area (1485.6 km²). The forest area outside the conservation area is under the jurisdiction of a division of forest offices. The Department of National Park and Wildlife Conservation (DNPWC) (077/78 Eco 45) and the National Trust for Nature Conservation, Annapurna Conservation Area Project (279/077/078) provided a research permit.

Data collection

The Government of Nepal (GoN) developed relief guidelines to assist local people with wildlife damage, including the leopard, in 2009 (*Acharya et al.*, 2016). We compiled compensation data for HLC (leopard attacks on livestock) between 2017 and 2020 from the Divisional Forest Offices (DFO) in Myagdi, Kaski, and Lamjung and Conservation Area Management Units (CAMU) in Bujhung, Sikles, Lwang, and Ghandruk. The data were managed following the Nepalese Calendar, which runs from mid-July to mid-July (Bikram Sambat), and we used fiscal years to ensure data consistency. Although there were cases

of leopards killing dogs and hens in the study area, we only recorded species for which compensation had been allocated to livestock owners by the government. Officials from the DFO and CAMU verified all reported data before compensation. Conflict information was gathered from 274 locations ("conflict sites" hereafter). In the study districts, we visited 252 conflict sites with elevations lower than 3,000 m. For the 22 conflict sites with elevations higher than 3,000 m, we used Google Earth Pro 7.3.3 and took help from local herders who were present during the conflict incident at the sites to identify the grid cell of the conflict site. The research team conducted field visits accompanied by staff from the DFO and CAMU of a particular village. The survey was conducted only after ethical approval from the DFO offices (Permission number: 1299) in each district and the CAMU offices inside conservation areas (Permission number: 279/077/078).

We located the owners who lost their livestock between 2017 and 2020 based on the information available from the compensation records. With the help of the livestock owners, we visited conflict sites. We recorded the GPS location of each site, along with information on the particular season and time of the incidents.

Data processing

Considering the limited resources, we had to maintain effectiveness by reducing the logistical complexity of the survey; hence, we stratified the study area into $4 \text{ km} \times 4 \text{ km}$ (i.e., 16 km^2) grids (n = 478) using ARC GIS 10.5 (ESRI, 2017). Out of 476 sampling grids, we recorded conflicts from 93 grids. The cell size was selected as $4 \text{ km} \times 4 \text{ km}$ to reduce chances of autocorrelation and identify landscape drivers of human–leopard conflicts. Studies (Naha, Sathyakumar & Rawat, 2018; Naha et al., 2020) have used $2 \text{ km} \times 2 \text{ km} - 5 \text{ km} \times 5 \text{ km}$ for the leopard conflict survey in previous studies. The grid size ($4 \text{ km} \times 4 \text{ km}$) was selected based on the topographic features of the study area, to increase survey precision, alongside decreasing survey cost and logistical complexity.

We examined various potential explanatory variables by utilizing publicly available data layers previously explored in human-leopard conflict studies (*Naha et al.*, 2020; *Ramesh et al.*, 2020; *Sharma et al.*, 2020; *Yadav et al.*, 2020; *Broekhuis, Cushman & Elliot*, 2017; *Rostro-García et al.*, 2016; *Treves et al.*, 2011). We compiled a comprehensive set of 14 landscape predictors for each grid cell, categorizing them into five distinct groups (Table 1).

We accessed land cover data specific to Nepal from *ESRI* (2020) to generate land use types within our study area. Subsequently, for each grid cell, we computed the areas corresponding to various land cover classes, including agricultural land, forests, bare ground, grassland, and shrubland. We applied the "Spatial join" tool in Arc GIS 10.5. We relied on Nepal's land cover data to assess water bodies within our study area. We extracted information regarding the river network from OCHA Nepal (*OCHA Nepal*, 2021a) and computed the lengths of rivers within each grid cell through the 'Intersect' function in Arc GIS. To determine the distance from water bodies to each grid cell, we employed the "Euclidean distance" tool.

Regarding roads and settlements, we obtained shape files representing Nepal's road network and settlements from OCHA Nepal (*OCHA Nepal*, *2021b*; *OCHA Nepal*, *2021c*).

Table 1 Major predictor variables considered for spatial analysis in the project sites.							
Types of variables	Predictor variable	Abbreviation	Unit	Range	Source		
Habitat variables	Area of agricultural land	AAL	m^2	0-3,177,300	ESRI (2020)		
	Area of bare ground	ABG	m^2	0-12,706,300			
	Area under forests	AF	m^2	0-15,947,900			
	Area of grassland	AGL	m^2	0-22,14,600			
	Area of shrubland	ASL	m^2	0-15,072,200			
Protected area	Distance from the protected area	DPA	meter (m)	0-42,554.9			
Water	Area of water bodies	AWB	m^2	0-2,974,900	ESRI (2020)		
	River length	RL	meter (m)	0-14,483.10	OCHA Nepal (2021a)		
	Distance to water bodies	DWB	meter (m)	0-8,594.57	OCHA Nepal (2021a)		
Human influence and infrastructure	Length of road	LR	meter (m)	0-107,248.5	OCHA Nepal (2021b)		
	Distance from road	DR	meter (m)		OCHA Nepal (2021c)		
	Distance from settlement	DS	meter (m)				
Topography	Slope		(°)	2.15-51.9	ASF, 2021		
	Elevation		meter(m)	415.1-7,420.4			

Using the Euclidean distance tool, we then calculated the distances from roads and settlements to each grid cell. Additionally, we assessed the lengths of roads within each grid cell using the 'Intersect' function in Arc GIS. We derived mean slope and elevation values for each grid from the Digital Elevation Model (DEM) file available on the Alaska Satellite Facility (ASF) website (*ASF*, *2021*). This process was facilitated by the 'zonal statistics' tool in ARC GIS. The nearest distance from protected areas boundary to the center of each grid cell was calculated for each grid using the Euclidean distance tool in Arc GIS. The points inside the protected area boundary were manually set as zero, the distance of points outside the boundary were calculated, and the datasets were merged to get the final distance value.

Data analysis

We also tested three additional temporal predictor variables for a relationship with leopard depredations, including time of day, month, and season. First, attacks were assigned to a time frame. We divided 24 h into four-hour intervals since the precise timing of livestock predation was unknown (12 AM–4 AM, 4 AM–8 AM, 8 AM–12 PM, 12 PM–4 PM, 4 PM–8 PM, 8 PM–12 AM). We also divided 12 months into three seasons of 4 months each (winter *i.e.*, November–February, summer, *i.e.*, March–June, monsoon, *i.e.*, July–October). Statistical data analysis was done in the R Statistical package v 4.0.4 (*R Core Team, 2021*). We also used a chi-square (χ^2) test to examine seasonal, monthly, and temporal variations in livestock depredation. To uncover more information about the features of kill sites, we divided the assigned predictors into groups (Table 2). Descriptive summaries based on month, season, and time of leopard attacks on livestock were calculated using the Pivot table function in Microsoft Excel 2013.

To model the spatial spread and extent of livestock depredation, we used the presence or absence of conflict as the response variable. We used a generalized linear model (GLM) that included 14 continuous variables as predictors (explanatory variables) with the binomial distribution respectively using the package 'Desctools' (*Signorell et al.*, 2019) and 'manipulate' (*Racine*, 2012). For binomial distribution, the presence/absence of the conflict

Variables	Classes	Frequency of attack (%)
Slope (°)	2–10	22
	10–20	30
	20–30	29
	30–40	13
	>40	6
Elevation (m)	415–1,000	28
	1,000–2,000	34
	2,000–3,000	27
	>3,000	11
Location	Outside conservation areas	49
	Inside conservation areas	51
Distance from road (m)	0-500	44
	500-1,000	23
	1,000–1,500	14
	1,500–2,000	6
	2,000–2,500	4
	>2,500	9
Distance from river (m)	0-500	42
	500-1,000	29
	1,000-1,500	17
	1,500–2,000	9
	2,000–2,500	2
	>2,500	1
Distance from settlement (m)	0–500	65
	500-1,000	21
	1,000–1,500	9
	1,500–2,000	2
	2,000–2,500	2
	>2,500	1

incidents (response variable) was recorded on a binary coding basis (1 = presence of a conflict incident in a grid, 0 = absence of a conflict incident in a grid). The absence of conflict was taken as the reference variable when running the models. We selected the GLM due to its suitability for modeling binary response data (*Fernandes et al.*, 2021) and its balance between simplicity and interpretability, aligning well with our research objectives. All the variables were standardized using Z transformation, ensuring that they were on the same scale for easier comparison of their contributions in the GLM. Before model construction, a multi-collinearity test was done for all the variables based on variance inflation factor (VIF) functions using the package 'faraway' (*Boomsma*, 2014). Since none of the variables showed any multi-collinearity (VIF value > 5), we used all the variables for model construction (*Chatterjee & Hadi*, 2013).

To select the most parsimonious model among the set of models, Akaike's Information Criterion (AIC) was performed (*Akaike*, 1973). Using the function 'dredge' under the package 'MuMIn' (*Barton*, 2009), all possible models were constructed and ranked based on small-sampled AICc (*Barton & Barton*, 2020). The final model was obtained by averaging the top candidate models (delta AIC \leq 2) (*Burnham & Anderson*, 2001). To test the predictive performance of the dominant model, we generated the receiver

Table 3 GLM model with the binomial structure for the probability of livestock predation by leopard.

	Estimate	Std. Error	z value	$\Pr(> \mathbf{z})$
(Intercept)	-2.75313	0.541284	-5.0863	3.65E-07
LR	0.243474	0.213269	1.141631	0.2536
RL	0.334842	0.163479	2.048231	0.0405
Slope	-0.59343	0.234312	-2.53266	0.0113
DPA	-0.37682	0.192787	-1.9546	0.0486
Elevation	1.144401	0.5124	2.233416	0.0255
DS	-1.16784	0.468449	-2.493	0.0127
DR	-0.3269	0.534292	-0.61183	0.5407
DWB	-0.40473	0.667943	-0.60594	0.5446
AF	0.503323	0.263548	1.909795	0.0462
AGL	-0.13252	0.247977	-0.53439	0.5931
AAL	0.333532	0.146614	2.274901	0.0229
ASL	-0.15425	0.235238	-0.6557	0.5120
ABG	-1.52401	1.225288	-1.24379	0.2136
AWB	0.100116	0.154925	0.646221	0.5181

Table 4 Second order Akaike Information criterion scores (AICc, ΔAIC & AIC weight) of a generalized linear model with binomial structure.

Component models*	df	AICc	ΔΑΙС	AIC weight	LogLik
Binomial distribution					
AAL+ABG+AF+DPA+DS+Elevation+RL+Slope	9	-162.742	343.9	0.00	0.018
AAL+ABG+AF+DPA+DS+RL+Slope	8	-164.005	344.3	0.44	0.014
AAL+ABG+AF+DPA+DS+Elevation+RL+LR+Slope	10	-162.168	344.8	0.94	0.011
AAL+ABG+AF+DPA+DR+DS+Elevation+RL+Slope	7	-165.405	345.1	1.17	0.010
AAL+AF+DPA+DR+DS+Elevation+RL+Slope	10	-162.433	345.4	1.47	0.008
AAL+ABG+AF+AWB+DPA+DS+Elevation+RL+Slope	10	-162.460	345.4	1.53	0.008
AAL+ABG+AF+AGL+DPA+DS+DWB+Elevation+RL+Slope	10	-162.570	345.6	1.75	0.007
AAL+ABG+AF+ASL+DPA+DS+Elevation+RL+Slope	10	-162.599	345.7	1.80	0.007
AAL+ABG+AF+AGL+DPA+DS+Elevation+RL+Slope	10	-162.646	345.8	1.90	0.007

operating characteristic (ROC) curve and area under the curve (AUC) value using the package 'ROCR' (*Sing et al.*, 2005). We obtained high model uncertainty among the selected predictors indicated by similar model weight. Thus, we did full model averaging (Table 3 and Table 4) to compute the effect of predictors. Additionally, we created an odds ratio plot to visualize the effect sizes of the predictors. The plot displayed the odds ratios with 95% confidence intervals, aiding in the interpretation of predictor variable impacts on the presence or absence of conflict incidents using the package 'ggplot 2' (*Wickham*, 2016).

We generated the conflict probability map through the maximum entropy (MaxEnt) modelling. MaxEnt is a widely used approach (*Fitzpatrick*, *Gotelli & Ellison*, 2013; *Phillips*, *Anderson & Schapire*, 2006), demonstrating the best predictive power across all sample sizes (*Elith et al.*, 2011; *Wisz et al.*, 2008). The occurrence points of conflict were filtered

by keeping at least 100 m of the distance between locations, thereby minimizing spatial autocorrelation (*Karki & Panthi, 2021*; *Adhikari et al., 2022*). For this purpose, the georeferenced points were spatially thinned using the SpThin package (*Aiello-Lammens et al., 2015*). Using this technique, we utilized the spatially filtered conflict occurrence points alongside the variables with high significance in the GLM models to predict the conflict probability in the study area (*Adhikari et al., 2022*). The MaxEnt program (version 3.4.4) was set up to use 70% of the data points for training and 30% for model validation. A maximum iteration limit of 1,000 was chosen, and models were replicated ten times to generate average model information (*Barbet-Massin et al., 2012*). We assessed the model accuracy through the threshold-independent (AUC-ROC) method and the threshold-dependent true skill statistics (TSS) method. AUC value ranges from 0 to 1. Similarly, TSS ranges from -1 to +1, with the model with a higher value in both representing good predictive performance (*Allouche, Tsoar & Kadmon, 2006*). The continuous probability map obtained from MaxEnt was reclassified in ArcGis 10.5 to obtain a distinct probability of conflict (low = <0.40, medium = 0.4–0.6, and high = >0.6).

RESULTS

Seasonal and temporal patterns of livestock predation

Livestock losses to leopards varied significantly with respect to season ($\chi 2 = 15.738$, df = 2, p-value < 0.001) and month ($\chi 2 = 28.665$, df = 11, p-value < 0.002). Winter exhibited the highest average count of approximately 37.00, suggesting a potential peak in livestock depredation during this season. Summer followed closely with an average count of approximately 34.33, while monsoon had the lowest average count of about 20.33. The standard errors for all three seasons were relatively consistent, indicating a similar level of variability in the counts within each season (Fig. 2). Similarly, there was also a significant difference in the timing of leopard attacks on livestock ($\chi 2 = 56.745$, df = 5, p-value < 0.001). The "4 PM to 8 PM" consistently recorded the highest average count, averaging approximately 30.33 livestock depredation, signifying a recurrent peak in the phenomenon during the late afternoon and early evening hours. Following closely, the "8 PM to 12 AM" exhibited a substantial average count of approximately 14.33, indicating continued activity during the evening and early night.

Conversely, the "12 PM to 4 PM" displayed a significantly lower average livestock depredation count, with an average of approximately 13.33. The time period between "8 AM to 12 PM" had a moderate average count of about 12.33, while the "12 AM to 4 AM" and "4 AM to 8 AM" had the lowest average counts, each hovering around 12.00, suggesting relatively low activity during the late night and early morning. The standard error values for each time period indicate the precision of the mean estimates and the extent to which the counts may vary within each specific time period (Fig. 2).

Livestock losses and characteristics of kill sites

During the three years, 439 livestock were reportedly killed by leopards in three districts. Goats (*Capra aegagrus hircus*) were the most predated livestock (66.5%), followed by sheep (*Ovis aries*) (22.5%), cows/oxen (*Bos taurus*) (7%), and buffalo (*Bubalus bubalis*)

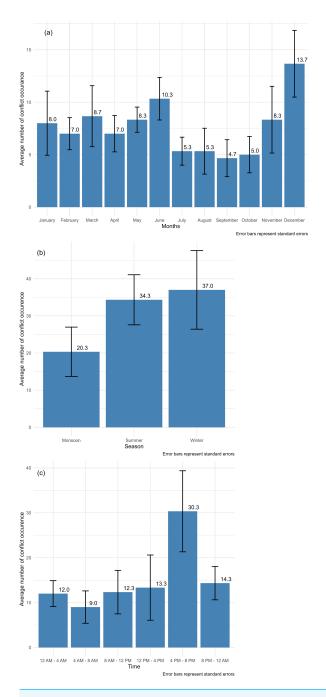


Figure 2 Mean count for (A) month, (B) season and (C) with error bars in the study area during 2017–2020.

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(4%). The analysis of data across slope and elevation revealed that about 80% of kill sites occurred within a 30-degree slope, and about 90% occurred within 3,000 m elevation. In inside conservation areas, there was a lower percentage of livestock depredation (41%) than in outside conservation areas (59%). It is apparent from the kill sites that about 65% of livestock depredation in the study area was recorded within 1 km of a road. The number

of livestock depredation events decreased with distance from roads. Similar patterns were observed when conflict locations were analyzed in relation to distance from rivers and settlements. About 70% of livestock depredation was observed within 1 km of a river and 85% within 1 km of a settlement (Table 2).

Influence of variables on leopard attack on livestock

In our study, we examined the significance of various variables regarding the presence or absence of livestock depredation by leopards. River length exhibited a significant positive association with livestock depredation ($\beta = 0.3348$; p = 0.0405), indicating that areas with longer rivers were more susceptible to leopard attacks on livestock. Additionally, slope displayed a significant negative relation with livestock depredation ($\beta = -0.5934$; p = 0.0113), suggesting that areas characterized by steeper terrain experienced fewer instances of leopard predation. The proximity to the protected area demonstrated a significant negative correlation with livestock depredation ($\beta = -0.3768$; $\beta = 0.0486$). This suggests that areas closer to protected areas experienced elevated risks of livestock depredation.

Moreover, elevation demonstrated a significant positive relation ($\beta = 1.1444$; p = 0.0255), implying that higher elevations were linked to an increased likelihood of leopard attacks on livestock. Furthermore, the forest area exhibited a significant positive relation with livestock depredation ($\beta = 0.5033$; p = 0.0462), indicating that larger forested areas heightened the risk of leopard predation. Similarly, the area of agricultural land demonstrated a significant positive association with livestock depredation ($\beta = 0.3335$; p = 0.0229), suggesting that larger agricultural areas were more vulnerable to leopard attacks on livestock. The distance to settlements variable exhibited a statistically significant negative relationship with livestock depredation ($\Re = -1.1678$; p = 0.0127) (Table 3). This suggests that areas closer to human settlements experienced a higher risk of leopard predation. The dominant model (GLM with binomial structure) had a receiver operating curve value of 0.85 (83.55% accuracy). We also generated an odds ratio plot to provide a visual representation of the effect sizes of our predictor variables. This plot displayed odds ratios along with their corresponding 95% confidence intervals, serving as a valuable tool for interpreting the impacts of these predictor variables on the presence or absence of conflict incidents (Fig. 3).

Among the nine different component models developed through model averaging (delta AIC \leq 2), the results of the GLM model with binomial structure (smallest AICc = -162.742) indicate that predictors such as the area of agricultural land, bare ground, forests, distance to protected areas and settlements, elevation, length of the river, and slope appeared as the dominant model for leopard attacks on livestock in the study area (Table 4.

Probability of conflict

A total of 289.11 km² (approximately 5% of the total study area) was considered high risk for livestock depredation by leopards. Kaski district had the largest high conflict-prone area (approximately 122.28 km²), followed by Lamjung (approximately 107.01 km²) and Myagdi (approximately 59.82 km²). Similarly, 18% of the high-risk area was incorporated

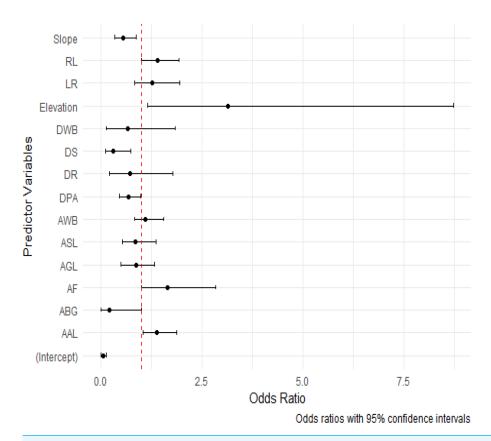


Figure 3 Odd ratios plot for predictor variables with 95% confidence intervals.

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within Annapurna CA (Fig. 4). The model accuracy was quite good, with an average AUC of 0.82 ± 0.09 and an average TSS 0.68 ± 0.08 .

DISCUSSION

Our study comprehensively analyzes the multifaceted interactions between leopards and livestock within our research area. By delving into various aspects of leopard predation patterns and the environmental factors that influence them, we aim to contribute significantly to understanding human-leopard conflicts and developing effective mitigation strategies.

Livestock depredation by leopards

This study revealed that leopards primarily preyed on goats, followed by sheep and cattle. This predation pattern aligns with the livestock population ratios in the study districts, as the Ministry of Agricultural and Livestock Development Nepal (*MOALD*, 2021) reported in 2021: 50% goats, 7% sheep, 29% cattle, and 14% buffalo. In contrast, sheep were the second most vulnerable prey livestock to leopards in the study area despite constituting the smallest proportion of the population compared to cattle and buffalo. Goats and sheep, as opposed to cattle and buffalo, exhibit less defensive behavior (*Dhungana et al.*, 2019), making them easier prey for leopards to capture. Although the diet of the leopard ranges

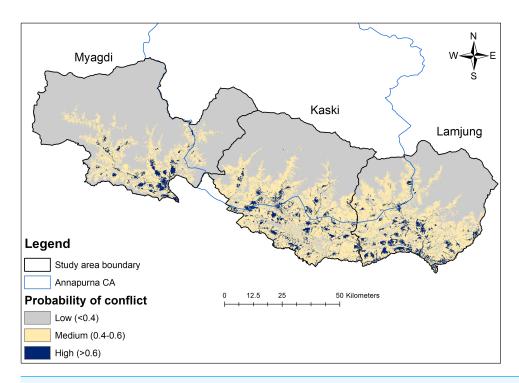


Figure 4 Leopard livestock predation risk map.

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mainly from small to some very large prey (>100 kg) (*Lovari, Ventimiglia & Minder, 2013*), they generally prefer species weighing between 10–40 kg (*Hayward et al., 2006*) and 2–25 kg (*Lovari, Ventimiglia & Minder, 2013*). As a result, they exhibit similar size preferences when preying on goats and sheep. Moreover, the lesser killing of cattle and buffalos in the study area might be attributed to their large body size, which is not preferred by leopards (*Lovari, Ventimiglia & Minder, 2013*; *Hayward et al., 2006*).

Seasonal and time-based variations in livestock depredation by leopards

Our analysis showed strong variations in livestock losses among seasons, months, and times. Most leopard attacks on livestock occur during the dry season (winter and summer). Our results coincide with studies conducted by *Naha et al.* (2020) in the Himalayan region of India and *Sijapati et al.* (2021) in the Terai region of Nepal. The dry season corresponds with the planting and harvesting of agricultural crops. During these months, farmers are busy with crop harvesting and production, leaving their livestock ranging freely (*Naha et al.*, 2020). Due to the cold temperatures in the winter, managing livestock guarding also becomes difficult for herders. Negligence by herders is regarded as one of the main contributing factors to livestock losses by predators (*Maclennan et al.*, 2009).

Moreover, the months of the winter season (November and December) receive less rainfall and thus require free grazing of livestock in forest areas due to the limited availability of fodder for stall feeding, making them more vulnerable to leopard attacks (*Dhungana et al.*, 2019). Several studies have reported leopard behavior as nocturnal (*Odden et al.*,

2014; Ahmed et al., 2012; Qamar et al., 2010). However, some studies also reported higher livestock depredation by leopards during the daytime (Naha et al., 2020; Woodroffe et al., 2007). In our study, the timing of leopard attacks on livestock also varied significantly, with peak occurrence during the evening time (4 PM–8 PM), similar to the studies conducted by Dar et al. (2009) at Machiara National Park, Pakistan. Multiple factors, such as animal husbandry practices and the availability of alternate prey, influence the timing of leopard depredation on livestock (Akrim et al., 2021). To sum up, our study emphasizes the significant impact of seasonality and daily timing on leopard predation of livestock, echoing findings from various regions. These insights underscore the complex interplay of factors, including animal husbandry practices and prey availability, in shaping the patterns of leopard attacks on livestock.

Factors influencing leopard predation on livestock

This study revealed that forest area, agricultural area, slope, distance to protected areas, distance to settlements, length of the river, and elevation affect livestock kills by leopards (Table 3). In India, the availability of water resources emerged as a spatial factor influencing leopard predation rates, as previously highlighted by Karanth et al. (2013). This observation resonates with similar research conducted in arid ecosystems of Africa, where water availability has consistently been identified as a primary driver of human-carnivore conflicts (Abade et al., 2018; Beattie et al., 2020). Our study corroborates these established findings. Specifically, we found a statistically significant positive correlation between the length of the river and the probability of livestock depredation by leopards. Rural villages heavily rely on livestock rearing as a prominent profession in our study area, which is characterized by higher-sloped geographical terrain and lush forests. Previous studies, such as Rostro-García et al. (2016), have reported leopard predation on livestock in rugged areas of Bhutan. Our study revealed a contrasting pattern where the probability of livestock depredation decreased with increasing slope. This finding can be attributed to the already prevalent sloped geographical terrain in our study area, which may act as a natural deterrent for leopards, making it more difficult to access and prey upon livestock. Interestingly, the study conducted by Rather, Kumar & Khan (2020) also observed high occurrences of leopards on gentle slopes, indicating that leopard behavior and habitat preferences can vary across different regions. These findings highlight the complexity of the relationship between slope and leopard predation and emphasize the need for further research to understand better the factors influencing livestock depredation in diverse geographical settings.

With increasing distance from protected areas, we observed a decreasing trend in leopard predation on livestock. Our findings are consistent with studies conducted by *Constant* (2014) in South Africa. However, *Naha et al.* (2020) documented contrasting results and found that conflicts with leopards were higher as they moved farther away from reserves. Factors such as habitat availability, prey availability, and local community dynamics can play significant roles in shaping the patterns of leopard predation on livestock. Further research is needed to understand the underlying mechanisms driving these variations and develop context-specific strategies for mitigating human-leopard conflicts.

This study revealed that elevation was a significant factor for leopard attacks on livestock, implying that higher elevations were linked to an increased likelihood of leopard attacks on livestock. Leopards can be found throughout Nepal, from the low-lying Terai (100 m) to the Himalayan peaks (4,000 m) (*Dhungana et al.*, 2019). This finding aligns with recent research conducted by *Baral et al.* (2023), which suggests that leopards are experiencing a shift in their habitat preferences in response to the effects of climate change. As temperature rises and ecosystems undergo transformations, leopards may be compelled to explore higher-elevation areas in search of suitable habitats and prey resources. Consequently, the increased presence of leopards at higher elevations may bring a higher incidence of livestock attacks in these regions.

In the rural villages inside the Annapurna Conservation Area (ACA), livestock grazing practices are prevalent throughout the year, with cattle sheds strategically positioned at different elevation ranges within the forest. This availability of prey, facilitated by the existing livestock husbandry practices, may be one of the reasons why the probability of leopard predation on livestock is positively associated with the forested area. The mid-hills region of Nepal has witnessed an increase in forest area in recent decades, which could further contribute to higher carnivore-related livestock depredations, as found by *Michalski et al.* (2006).

Despite this trend, studies have also shown that leopards exhibit adaptability to human-modified landscapes (*Baral et al.*, 2021; *Odden et al.*, 2014; *Constant, Bell & Hill*, 2015). A study conducted by *Bista et al.* (2022) in Nepal's Kathmandu district further strengthens this assertion, revealing a substantial leopard presence in areas characterized by high human population densities. This underscores the leopard's capacity to thrive in proximity to human settlements. Furthermore, the settlements in our study area are mostly scattered and not so densely populated, allowing leopards to dwell nearby. This adaptability, in conjunction with the easy availability of livestock near the settlements, likely contributes to the observed increase in livestock depredation with a decrease in distance from settlements.

Our findings support a positive association between livestock depredation and agricultural land, consistent with previous studies by Kshettry, Vaidyanathan & Athreya (2018) and Kabir et al. (2014), which reported higher leopard predation on livestock in human-use landscapes, especially in areas with agricultural activities. Agricultural lands provide a potential food source for leopards, including domestic livestock like cattle, buffalo, goats, and chickens. The remarkable adaptive nature of leopards (Bista et al., 2022) allows them to exploit these human-modified habitats for hunting and acquiring additional food resources. Kshettry, Vaidyanathan & Athreya (2018) even reported a higher contribution of livestock to the leopard diet from human-use landscapes. The ability of leopards to cover large home ranges and their highly adaptive nature (Abade et al., 2018) enables them to persist in areas with varying degrees of human presence (Odden, Wegge & Fredriksen, 2010). Despite their adaptive behaviors, leopards may avoid areas with higher human settlement density due to potential conflicts and increased human activity, thereby limiting their predation on livestock in such regions. Hence, our results suggest that while leopards may exploit agricultural land for hunting opportunities, they may also exhibit caution and avoid areas with denser human populations. This dual pattern intricate interplay of

ecological and behavioral factors underscores the complex dynamics of human-leopard interactions, necessitating further research on spatial dynamics of settlements and their impact on human-leopard conflicts.

CONCLUSION

Our findings offer valuable insights for managing human-leopard conflicts in the study area and beyond. The conflict risk maps generated are instrumental in pinpointing high-risk regions where resources and policy changes can be strategically directed. Key mitigation strategies include enhancing corral structures, reinforcing stock guarding, and discouraging livestock grazing in vulnerable areas. Collaborative efforts among stakeholders are essential for successful coexistence between communities and leopards. Effective guarding is crucial in the winter and summer months, especially in December and March when leopard attacks on cattle are at their worst. Building safer or predator-proof corrals and emphasizing stall-feeding techniques, particularly in locations with forest fringes, are necessary. It is also necessary to avoid grazing livestock inside dense forests and near water bodies. If grazing is unavoidable in such areas, we advise using communally coordinated herding practices. Developing a conflict mitigation strategy that incorporates cooperation between divisional forest offices, local populations, and conservationists will be essential to encourage coexistence between people and leopards. We recommend a detailed and extensive study to understand the habitat utilization pattern of leopards at a finer scale through intensive camera trapping and radio telemetry methods in the study area.

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Competing Interests

Bikram Shrestha is a general member of Green Governance Nepal and employee of Department of Biodiversity Research, Global Change Research Institute, Czech Academy of Sciences, Brno, Czech Republic.

Author Contributions

- Saurav Lamichhane conceived and designed the experiments, performed the experiments, prepared figures and/or tables, authored or reviewed drafts of the article, identified funding agency, and approved the final draft.
- Divya Bhattarai conceived and designed the experiments, performed the experiments, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Tek Maraseni performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Kyle J. Shaney performed the experiments, authored or reviewed drafts of the article, and approved the final draft.
- Jhamak Bahadur Karki performed the experiments, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Binaya Adhikari analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Pratik Pandeya analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- Bikram Shrestha analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- Hari Adhikari conceived and designed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

Field experiments were approved by the Department of Forest and Watershed Management (Permission number: 279/077/078).

Data Availability

The following information was supplied regarding data availability: The raw measurements are available in the Supplementary Files.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.16516#supplemental-information.

REFERENCES

- **Abade L, Cusack J, Moll RJ, Strampelli P, Dickman AJ, Macdonald DW, Montgomery RA. 2018.** Spatial variation in leopard (Panthera pardus) site use across a gradient of anthropogenic pressure in Tanzania's Ruaha landscape. *PLOS ONE* **13(10)**:e0204370 DOI 10.1371/journal.pone.0204370.
- Acharya KP, Paudel PK, Jnawali SR, Neupane PR, Koehl M. 2017. Can forest fragmentation and configuration work as indicators of human-wildlife conflict? Evidences from human death and injury by wildlife attacks in Nepal. *Ecological Indicators* 80:74–83 DOI 10.1016/j.ecolind.2017.04.037.
- **Acharya KP, Paudel PK, Neupane PR, Köhl M. 2016.** Human-wildlife conflicts in Nepal: patterns of human fatalities and injuries caused by large mammals. *PLOS ONE* **11(9)**:e0161717 DOI 10.1371/journal.pone.0161717.
- Adhikari B, Baral K, Bhandari S, Szydlowski M, Kunwar RM, Panthi S, Neupane B, Koirala RK. 2022. Potential risk zone for anthropogenic mortality of carnivores in Gandaki Province, Nepal. *Ecology and Evolution* 12(1):e8491 DOI 10.1002/ece3.8491.
- Ahmed RA, Prusty K, Jena J, Dave C, Das SK, Sahu HK, Rout SD. 2012. Prevailing human carnivore conflict in Kanha-Achanakmar corridor, Central India. *World Journal of Zoology* **7(2)**:158–164 DOI 10.5829/idosi.wjz.2012.7.2.6335.
- Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38(5):541–545 DOI 10.1111/ecog.01132.
- **Akaike H. 1973.** Information theory and an extension of the maximum likelihood principle. In: *Proceedings of the 2nd international symposium on information*. Budapest: Akademiai Kiado.
- Akrim F, Mahmood T, Belant JL, Nadeem MS, Qasim S, Zangi IUD, Asadi MA. 2021. Livestock depredations by leopards in Pir Lasura National Park, Pakistan: characteristics, control and costs. *Wildlife Biology* 2021(1):1–7 DOI 10.2981/wlb.00782.
- Alaska Satellite Facility (ASF). 2021. Available at https://asf.alaska.edu (accessed on 30 April 2022).
- **Allouche O, Tsoar A, Kadmon R. 2006.** Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* **43(6)**:1223–1232 DOI 10.1111/j.1365-2664.2006.01214.x.
- Athreya V, Odden M, Linnell JDC, Karanth KU. 2011. Translocation as a tool for mitigating conflict with leopards in human-dominated landscapes of India. *Conservation Biology* 25(1):133–141 DOI 10.1111/j.1523-1739.2010.01599.x.
- Baral K, Adhikari B, Bhandari S, Kunwar RM, Sharma HP, Aryal A, Ji W. 2023. Impact of climate change on distribution of common leopard (Panthera pardus) and its implication on conservation and conflict in Nepal. *Heliyon* **9**(5):e12807 DOI 10.1016/j.heliyon.2023.e12807.
- Baral K, Sharma HP, Rimal B, Thapa-Magar K, Bhattarai R, Kunwar RM, Aryal A, Ji W. 2021. Characterization and management of human-wildlife conflicts in mid-hills

- outside protected areas of Gandaki province, Nepal. *PLOS ONE* **16(11)**:e0260307 DOI 10.1371/journal.pone.0260307.
- Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* 3(2):327–338 DOI 10.1111/j.2041-210X.2011.00172.x.
- **Barton K. 2009.** MuMIn: multi-model inference. R Package Version 0.12.2/r18. *Available at http://R-Forge.R-project.org/projects/mumin/*.
- **Barton K, Barton MK. 2020.** MuMIn: multi-model inference. R package version 1.43.17. Version 1, 18. *Available at https://CRAN.R-project.org/package=MuMIn.*
- **Beattie K, Olson ER, Kissui B, Kirschbaum A, Kiffner C. 2020.** Predicting livestock depredation risk by African lions (Panthera leo) in a multi-use area of northern Tanzania. *European Journal of Wildlife Research* **66**:1–14 DOI 10.1007/s10344-019-1348-5.
- **Bista A, Chanchani P, Subedi N, Bajracharya SB. 2022.** The peri-urban leopards of Kathmandu: assessing determinants of presence and predation on domestic animals. *Oryx* **56(1)**:91–100.
- **Boomsma A. 2014.** *Regression diagnostics with R. Regrdiag R.tEx.* Department of Statistics & Measurement Theory. University of Groningen, Groningen Netherlands, 22.
- **Broekhuis F, Cushman SA, Elliot NB. 2017.** Identification of human—carnivore conflict hotspots to prioritize mitigation efforts. *Ecology and Evolution* **7**:10630–10639.
- **Burnham KP, Anderson DR. 2001.** Kullback—Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* **28**:111–119 DOI 10.1071/WR99107.
- **Chatterjee S, Hadi AS. 2013.** *Regression analysis by example.* 5th edition. New York: Wiley, 98.
- **Constant N. 2014.** A socio-ecological approach towards understanding conflict between leopards (Panthera pardus) and humans in South Africa: implications for leopard conservation and farming livelihoods. Doctoral dissertation, Durham University.
- Constant NL, Bell S, Hill RA. 2015. The impacts, characterisation and management of human—leopard conflict in a multi-use land system in South Africa. *Biodiversity and Conservation* 24(12):2967–2989 DOI 10.1007/s10531-015-0989-2.
- **Dalerum F, Selby LO, Pirk CW. 2020.** Relationships between livestock damages and large carnivore densities in Sweden. *Frontiers in Ecology and Evolution* **7**:507 DOI 10.3389/fevo.2019.00507.
- Dar NI, Minhas RA, Zaman Q, Linkie M. 2009. Predicting the patterns, perceptions and causes of human—carnivore conflict in and around Machiara National Park, Pakistan. *Biological Conservation* 142(10):2076–2082 DOI 10.1016/j.biocon.2009.04.003.
- Dheer A, Davidian E, Courtiol A, Bailey LD, Wauters J, Naman P, Shayo V, Höner OP. 2022. Diurnal pastoralism does not reduce juvenile recruitment nor elevate allostatic load in spotted hyenas. *Journal of Animal Ecology* 91(11):2289–2300 DOI 10.1111/1365-2656.13812.
- Dhungana R, Lamichhane BR, Savini T, Dhakal M, Poudel BS, Karki JB. 2019. Live-stock depredation by leopards around Chitwan national park, Nepal. *Mammalian Biology* **96**(1):7–13 DOI 10.1016/j.mambio.2019.03.006.

- **DNPWC. 2017.** *Profiling of protected and human wildlife conflicts associated wild animals in Nepal.* Kathmandu: Department of National Parks and Wildlife Conservation.
- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17(1):43–57 DOI 10.1111/j.1472-4642.2010.00725.x.
- **ESRI. 2017.** *ArcGIS desktop: release 10.5.* Redlands, California: Environmental Systems Research Institute.
- **ESRI. 2020.** Sentinel-2 10-meter land use/land cover. *Available at https://livingatlas.arcgis.com/landcover/* (accessed on 22 May 2022).
- Fernandes AAT, Figueiredo Filho DB, Rocha ECD, Nascimento WDS. 2021. Read this paper if you want to learn logistic regression. *Revista de Sociologia e Politica* 28:006 DOI 10.1590/1678-987320287406en.
- **Fitzpatrick MC, Gotelli NJ, Ellison AM. 2013.** MaxEnt versus MaxLike: empirical comparisons with ant species distributions. *Ecosphere* **4**(**5**):1–15 DOI 10.1890/ES13-00066.1.
- **Graham K, Beckerman AP, Thirgood S. 2005.** Human—predator—prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* **122(2)**:159–171 DOI 10.1016/j.biocon.2004.06.006.
- Hayward MW, Henschel P, O'Brien J, Hofmeyr M, Balme G, Kerley GI. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* 270(2):298–313 DOI 10.1111/j.1469-7998.2006.00139.x.
- Inskip C, Zimmermann A. 2009. Human-felid conflict: a review of patterns and priorities worldwide. *Oryx* 43(1):18–34 DOI 10.1017/S003060530899030X.
- Jacobson AP, Gerngross P, Lemeris Jr JR, Schoonover RF, Anco C, Breitenmoser-Würsten C, Durant SM, Farhadinia MS, Henschel P, Kamler JF, Laguardia A, Rostro-García S, Stein AB, Dollar L. 2016. Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ* 4:e1974 DOI 10.7717/peerj.1974.
- Jnawali SR, Baral HS, Lee S, Acharya KP, Upadhyay GP, Pandey M, Shrestha R, Joshi D, Laminchhane BR, Griffiths J, Khatiwada AP, Subedi N, Amin R (compilers) 2011. The status of Nepal mammals. The National Red List Series, Department of National Parks and Wildlife Conservation, Kathmandu, Nepal. Available at https://www.researchgate.net/publication/258516080_The_Status_of_Nepal_Mammals_The_National_Red_List_Series_Department_of_National_Parks_and_Wildlife_Conservation_Kathmandu_Nepal (accessed on 13 October 2023).
- **Kabir M, Ghoddousi A, Awan MS, Awan MN. 2014.** Assessment of human—leopard conflict in Machiara National Park, Azad Jammu and Kashmir, Pakistan. *European Journal of Wildlife Research* **60**:291–296 DOI 10.1007/s10344-013-0782-z.
- Kandel SR, Neupane B, Miya MS, Sadadev BM, Khatri ND, Dhami B. 2023. An emerging issue of human-leopard conflict in the human-dominated landscape of mid-hills: a case study from Tanahun District of Nepal. *International Journal of Zoology* 2023:5690289 DOI 10.1155/2023/5690289.

- **Karanth KK, Gopalaswamy AM, Prasad PK, Dasgupta S. 2013.** Patterns of human—wildlife conflicts and compensation: insights from Western Ghats protected areas. *Biological Conservation* **166**:175–185 DOI 10.1016/j.biocon.2013.06.027.
- **Karki A, Panthi S. 2021.** Factors affecting livestock depredation by snow leopards (*Panthera uncia*) in the Himalayan region of Nepal. *PeerJ* **9**:e11575 DOI 10.7717/peerj.11575.
- **Karki J, Rawat G. 2014.** Human-leopard conflict in Nepal: a case study from Baitadi District. DNPWC, 2014. In: *Special issues on biodiversity conservation efforts in Nepal.* Kathmandu: Department of National Parks and Wildlife Conservation.
- **Koirala RK, Aryal A, Parajuli A, David A. 2012.** Human-common leopard (*Panthera pardus*) conflict in lower belt of Annapurna Conservation Area, Nepal. *Journal of Research in Conservation Biology* **1:**005–012.
- **Kshettry A, Vaidyanathan S, Athreya V. 2018.** Diet selection of Leopards (*Panthera pardus*) in a human-use landscape in North-Eastern India. *Tropical Conservation Science* **11**:1940082918764635 DOI 10.1177/1940082918764635.
- **Lamichhane BR, Lamichhane S, Regmi R, Dhungana M, Thapa SK, Prasai A, Gurung A, Bhattarai S, Paudel RP, Subedi N. 2021.** Leopard (Panthera pardus) occupancy in the Chure range of Nepal. *Ecology and Evolution* **11(20)**:13641–13660 DOI 10.1002/ece3.8105.
- Lamichhane BR, Persoon GA, Leirs H, Poudel S, Subedi N, Pokheral CP, Bhattarai S, Thapaliya BP, de Iongh HH. 2018. Spatio-temporal patterns of attacks on human and economic losses from wildlife in Chitwan National Park, Nepal. *PLOS ONE* 13(4):e0195373 DOI 10.1371/journal.pone.0195373.
- Lovari S, Ventimiglia M, Minder I. 2013. Food habits of two leopard species, competition, climate change and upper treeline: a way to the decrease of an endangered species? *Ethology Ecology & Evolution* 25(4):305–318

 DOI 10.1080/03949370.2013.806362.
- Maclennan SD, Groom RJ, Macdonald DW, Frank LG. 2009. Evaluation of a compensation scheme to bring about pastoralist tolerance of lions. *Biological Conservation* 142(11):2419–2427 DOI 10.1016/j.biocon.2008.12.003.
- Mateo-Tomás P, Olea PP, Sánchez-Barbudo IS, Mateo R. 2012. Alleviating human—wildlife conflicts: identifying the causes and mapping the risk of illegal poisoning of wild fauna. *Journal of Applied Ecology* 49(2):376–385
 DOI 10.1111/j.1365-2664.2012.02119.x.
- Michalski F, Boulhosa RLP, Faria A, Peres CA. 2006. Human—wildlife conflicts in a fragmented Amazonian Forest landscape: determinants of large felid depredation on livestock. *Animal Conservation* 9(2):179–188 DOI 10.1111/j.1469-1795.2006.00025.x.
- **Miller JR. 2015.** Mapping attack hotspots to mitigate human—carnivore conflict: approaches and applications of spatial predation risk modeling. *Biodiversity and Conservation* **24(12)**:2887–2911 DOI 10.1007/s10531-015-0993-6.
- MOALD. 2021. Livestock statistics of Nepal (2019/2020): Hariharbhawan, Lalitpur, Nepal. Available at https://www.dls.gov.np/downloadfiles/Livestock_Statistics_of_Nepal_2077_78_1659524236-1669717523.pdf.

- Naha D, Dash SK, Chettri A, Chaudhary P, Sonker G, Heurich M, Rawat GS, Sathyakumar S. 2020. Landscape predictors of human—leopard conflicts within multi-use areas of the Himalayan region. *Scientific Reports* 10(1):1–12 DOI 10.1038/s41598-020-67980-w.
- Naha D, Sathyakumar S, Rawat GS. 2018. Understanding drivers of human-leopard conflicts in the Indian Himalayan region: spatio-temporal patterns of conflicts and perception of local communities towards conserving large carnivores. *PLOS ONE* 13(10):e0204528 DOI 10.1371/journal.pone.0204528.
- NTNC (National Trust for Nature Conservation). 2018. Annual report 2018. NTNC: Khumaltar, Lalitpur, Nepal. *Available at https://www.ntnc.org.np/sites/default/files/doc_publication/2019-10/NTNC%20Annual_Report%202018.pdf*.
- **OCHA Nepal. 2021a.** Nepal road network. Humanitarian Data Exchange. *Available at https://data.humdata.org/dataset/nepal-watercourses-rivers* (accessed on 28 March 2022).
- **OCHA Nepal. 2021b.** Road network for Nepal. Humanitarian Data Exchange. *Available at https://data.humdata.org/dataset/nepal-road-network* (accessed on 28 March 2022).
- **OCHA Nepal. 2021c.** Settlements in Nepal. Humanitarian Data Exchange. *Available at https://data.humdata.org/dataset/settlements-in-nepal* (accessed on 28 March 2022).
- Odden M, Athreya V, Rattan S, Linnell JD. 2014. Adaptable neighbours: movement patterns of GPS-collared leopards in human dominated landscapes in India. *PLOS ONE* 9(11):e112044 DOI 10.1371/journal.pone.0112044.
- Odden M, Wegge P, Fredriksen T. 2010. Do tigers displace leopards? If so, why? *Ecological Research* 25(4):875–881 DOI 10.1007/s11284-010-0723-1.
- Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190(3–4):231–259 DOI 10.1016/j.ecolmodel.2005.03.026.
- **Puri M, Srivathsa A, Karanth KK, Patel I, Kumar NS. 2020.** The balancing act: maintaining leopard-wild prey equilibrium could offer economic benefits to people in a shared forest landscape of central India. *Ecological Indicators* **110**:105931 DOI 10.1016/j.ecolind.2019.105931.
- Qamar QZ, Dar NI, Ali U, Minhas RA, Ayub J, Anwar M. 2010. Human—leopard conflict: an emerging issue of common leopard conservation in Machiara National Park, Azad Jammu and Kashmir, Pakistan. *Pakistan Journal of Wildlife* 1:50–56 DOI 10.3724/SP.J.1141.2010.01035.
- **R Core Team. 2021.** R: a language and environment for statistical computing. Vienna: R Foundation for statistical Computing. *Available at https://www.R-project.org/*.
- **Racine J. 2012.** Rstudio: a platform-independent IDE for R and sweave. *Journal of Applied Economics* **27**:167–172.
- Ramesh T, Kalle R, Milda D, Gayathri V, Thanikodi M, Ashish K, Giordano AJ. 2020.

 Patterns of livestock predation risk by large carnivores in India's Eastern and

 Western Ghats. *Global Ecology and Conservation* 24:e01366.

- Rather TA, Kumar S, Khan JA. 2020. Multi-scale habitat modelling and predicting change in the distribution of tiger and leopard using random forest algorithm. *Scientific Reports* 10(1):1–19 DOI 10.1038/s41598-020-68167-z.
- Rostro-García S, Tharchen L, Abade L, Astaras C, Cushman SA, Macdonald DW. 2016. Scale dependence of felid predation risk: identifying predictors of livestock kills by tiger and leopard in Bhutan. *Landscape Ecology* 31(6):1277–1298 DOI 10.1007/s10980-015-0335-9.
- Sharma P, Chettri N, Uddin K, Wangchuk K, Joshi R, Tandin T, Pandey A, Gaira KS, Basnet K, Wangdi S, Dorji T. 2020. Mapping human-wildlife conflict hotspots in a transboundary landscape, Eastern Himalaya. *Global Ecology and Conservation* 24:e01284 DOI 10.1016/j.gecco.2020.e01284.
- Shehzad W, Nawaz MA, Pompanon F, Coissac E, Riaz T, Shah S, Taberlet P. 2015. Forest without prey: livestock sustain a leopard Panthera pardus population in Pakistan. *Oryx* 49(2):248–253 DOI 10.1017/S0030605313001026.
- Shrestha B, Khatri TB, Rana DB, Karki JB, Kindlmann P. 2022. Snow leopard-human conflict and effectiveness of mitigation measures. In: *Snow Leopards in Nepal: predator-prey system on the top of the world.* Cham: Springer International Publishing, 177–201 DOI 10.1007/978-3-031-11355-0_8.
- Signorell A, Aho K, Alfons A, Anderegg N, Aragon T, Arppe A, Baddeley A, Barton K, Bolker B, Borchers HW. 2019. DescTools: tools for descriptive statistics (Version 0.99 28). Available at https://CRAN.R-project.org/package=DescTools.
- Sijapati RK, Sharma HP, Sharma S, Subedi JR, Belant JL. 2021. Livestock depredation by Leopards and Tigers near Bardia National Park, Nepal. *Animals* 11(7):1896 DOI 10.3390/ani11071896.
- Sing T, Sander O, Beerenwinkel N, Lengauer T. 2005. ROCR: visualizing classifier performance in R. *Bioinformatics* 21(20):3940–3941.
- Stein AB, Athreya V, Gerngross P, Balme G, Henschel P, Karanth U, Miquelle D, Rostro-Garcia S, Kamler JF, Laguardia A, Khorozyan I. 2016. Panthera pardus. *The IUCN Red List of Threatened Species* 2016:e.T15954A102421779 DOI 10.2305/IUCN.UK.2016-1.RLTS.T15954A50659089.en.
- **Torres DF, Oliveira ES, Alves RR. 2018.** Conflicts between humans and terrestrial vertebrates: a global review. *Tropical Conservation Science* **11**:1940082918794084 DOI 10.1177/1940082918794084.
- **Treves A, Karanth KU. 2003.** Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* **17**:1491–1499 DOI 10.1111/j.1523-1739.2003.00059.x.
- **Treves A, Martin KA, Wydeven AP, Wiedenhoeft JE. 2011.** Forecasting environmental hazards and the application of risk maps to predator attacks on livestock. *BioScience* **61(6)**:451–458 DOI 10.1525/bio.2011.61.6.7.
- Venumière-Lefebvre CC, Breck SW, Crooks KR. 2022. A systematic map of human-carnivore coexistence. *Biological Conservation* 268:109515

 DOI 10.1016/j.biocon.2022.109515.

- **Wickham H. 2016.** ggplot2: elegant graphics for data analysis. New York: Springer-Verlag. *Available at https://ggplot2.tidyverse.org/*.
- Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A, NCEAS Predicting Species Distributions Working Group. 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14(5):763–773 DOI 10.1111/j.1472-4642.2008.00482.x.
- Woodroffe R, Frank LG, Lindsey PA, Mole Ranah S, Romañach S. 2007. Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: a case—control study. *Biodiversity and Conservation* 16(5):1245–1260 DOI 10.1007/s10531-006-9124-8.
- Yadav N, Areendran G, Sarma K, Raj K, Sahana M. 2020. Susceptibility assessment of human—leopard conflict in Aravalli landscape of Haryana using geospatial techniques. *Modeling Earth Systems and Environment* **7(3)**:1459–1473 DOI 10.1007/s40808-020-00858-y.