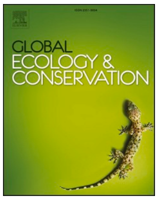
Global Ecology and Conservation 68 (2026) e04240

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco



Original research article

Leopard occupancy and habitat use in the multi-use Chitwan-Annapurna Landscape, Nepal

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ARTICLE INFO

Keywords:
Leopard
Human-dominated landscapes
Habitat use
Native prey
Occupancy modeling
Multi-use landscapes

ABSTRACT

We estimated leopard (*Panthera pardus fusca*) occupancy in a multi-use region within Nepal’s Chitwan-Annapurna Landscape to evaluate leopard habitat use and inform conservation planning in areas where most of the species’ habitat occurs outside protected areas. In 2021, sign surveys were conducted along 1277 km of transects distributed among 145 grid cells of 7×7 km within a 7105 km^2 study area, where 226 leopard signs (pugmarks and scats) were documented. We used an occupancy modeling framework to evaluate the influence of environmental and anthropogenic factors on leopard habitat use. We found that leopard occupancy ($\psi = 0.73 \pm 0.17$ CI) was strongly and positively associated with areas used by wild prey such as red muntjac (*Muntiacus muntjak*), rhesus macaques (*Macaca mulatta*), chital (*Axis axis*), and wild boars (*Sus scrofa*). Our results provide evidence that large carnivores like leopards can persist in human-dominated landscapes when native prey remains abundant, underscoring the need for community-based conservation that sustains both prey and predator populations beyond protected areas. By estimating leopard occupancy outside of protected areas, the research establishes a baseline for developing management strategies to ensure the continued existence of leopards in Nepal's multi-use landscapes.

1. Introduction

Large carnivores play critical roles in the structure and function of ecosystems, yet they are threatened globally (Hovardas et al., 2021), with many species experiencing dramatic population declines and range contractions (Ripple et al., 2016). Declines have been attributed to the combined pressures of habitat loss, poaching, declining prey, and persecution due to conflict with humans (Karanth and Chellam, 2009). Despite these challenges, some large carnivore populations have recovered in recent decades, notably, in the

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https://doi.org/10.1016/j.gecco.2026.e04240
Received 11 December 2025; Received in revised form 25 April 2026; Accepted 5 May 2026

human-dominated landscapes of Europe (Chapron et al., 2014) and South Asia (Lamichhane et al., 2018; Jhala et al., 2021). These recoveries in multi-use human-modified landscapes have challenged longstanding assumptions regarding the pristine habitat requirements of large carnivores (e.g. Mech, 1996). Considering the planetary-scale effect of human modification of landscapes, with over 95% of the globe's land being modified by humans (Theobald et al., 2020) and projections of human populations to increase up to 12 billion by 2100 (Gerland et al., 2014), there is a pressing need to understand patterns of large carnivore habitat use in human-modified landscapes to inform future carnivore conservation efforts globally.

Due to their trophic position, large carnivores typically occur at low density and display wide-ranging behaviors, resulting in expansive space requirements for population persistence (Linnell et al., 2008). The requirement for large landscapes contrasts with the global trend of diminishing “wilderness” spaces (Watson et al., 2016), making it challenging for large carnivore populations to exist solely within protected areas (Linnell et al., 2001). Instead, they must navigate fragmented multi-use landscapes that are heavily utilized by humans (Holland et al., 2018; Habib et al., 2021; Carter et al., 2023).

Big cats (*Panthera spp.)* are among the most iconic and threatened large carnivores worldwide (Macdonald & Loveridge, 2010). Large felids are hypercarnivores, relying primarily on large prey due to their energetic constraints (Carbone et al., 1999). This specialized diet poses challenges for adapting to multi-use landscapes where more generalist carnivores often thrive (Chapron et al., 2014). Leopards (*Panthera pardus*) are noted for their adaptability among big cats, demonstrating the capacity to inhabit diverse landscapes across Africa and Asia (Odden and Wegge, 2005; Odden et al., 2014; Athreya et., al., 2015; Kshettry et al., 2017; Gubbi et al., 2020). Leopards have the broadest dietary niche among the big cats, primarily preferring medium-sized prey (mean body weight < 25 kg, Hayward et al., 2006). This dietary flexibility enables leopards to exploit a variety of species including wild ungulates, livestock, and free-ranging dogs (Aryal et al., 2009; Athreya et al., 2014; Shehzad et al., 2015; Kshettry et al., 2018; Kandel et al., 2020; Puri et al., 2020), which enhances their adaptability to different ecosystems. The ability of leopards to coexist with humans in densely populated regions highlights the complex dynamics between large carnivore occurrence and human development (Braczkowski et al., 2018), an aspect that remains little studied and poorly understood. Approximately 83% of the leopard’s extant global range occurs in multi-use landscapes outside protected areas (Jacobson et al., 2016), underscoring the importance of understanding leopard habitat use and ecology beyond the borders of protected areas (Stein et al., 2020). However, the traits of low density and wide-ranging behavior present substantial challenges when attempting to understand fundamental aspects of large carnivore ecology, such as

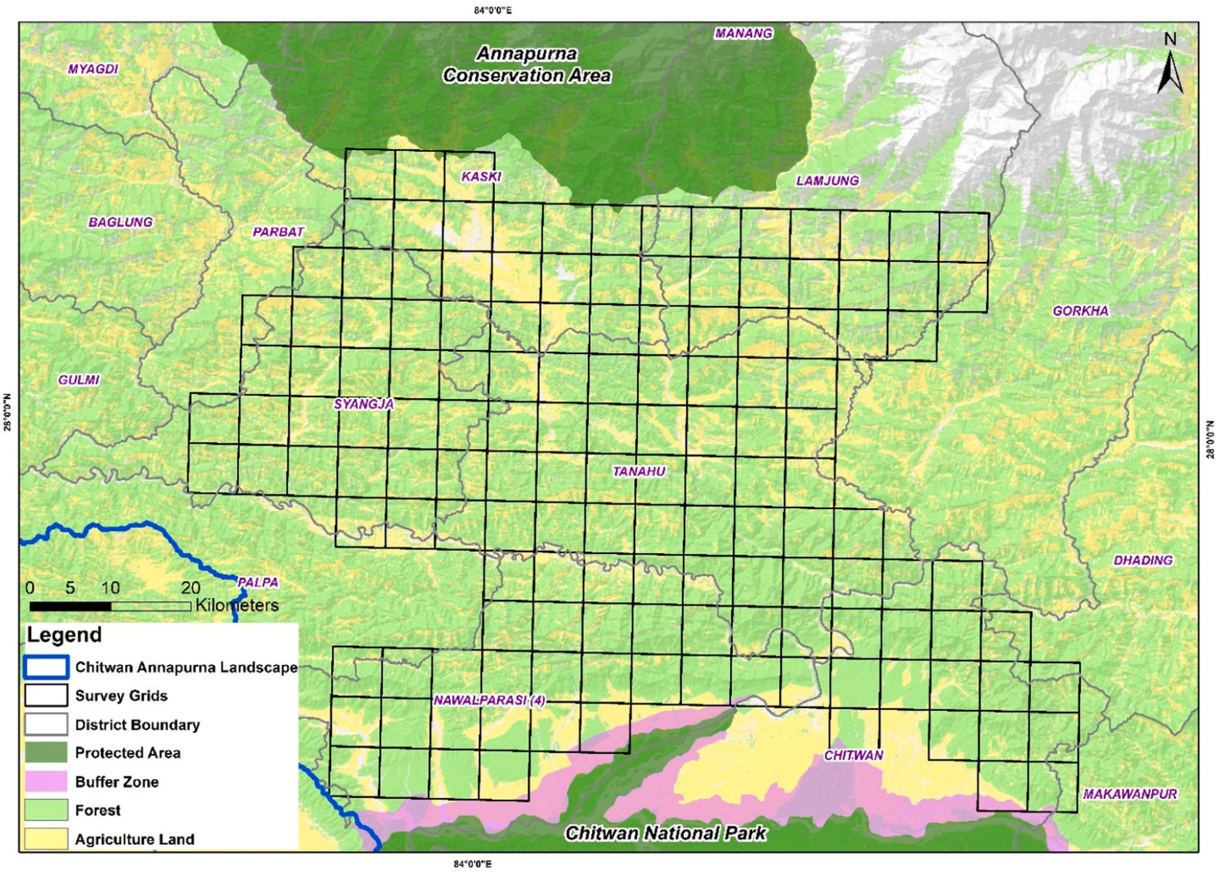

Fig. 1. Chitwan Annapurna Landscape (CHAL), Nepal, and 145 sample units where sign surveys were conducted in 2021 for leopard (*Panthera pardus fusca*) occupancy estimation.

abundance and habitat use at spatial scales relevant for effective management and conservation (Karanth et al., 2011).

Recent advancements in hierarchical modeling have revolutionized wildlife population studies by tackling the ubiquitous issues of observation error and heterogeneity in detection (Kery and Royle, 2015; 2020). The choice of the specific modeling framework depends on project objectives, spatial and temporal scales of interest, and available resources (Yoccoz, Nichols and Boulinier, 2001; Twining et al., 2022). Spatial-capture recapture (SCR) models (Royle et al., 2014) provide robust abundance estimates but are often cost-prohibitive for large-scale studies of large carnivores due to their reliance on detection data that includes the individual identity of animals (Seidlitz et al., 2021). Non-invasive survey methods such as non-invasive genetic sampling and camera trapping have increased our ability to monitor carnivores at large scales (Long et al., 2008), yet challenges remain in obtaining sufficient data for SCR in many wildlife management contexts. The use of occupancy as a surrogate for abundance has become widespread (MacKenzie et al., 2006) and can be highly effective for species and scenarios where occupancy-abundance relationships may be relatively linear (Linden et al., 2017; Fuller et al., 2022). Occupancy models leverage detection/non-detection data in a hierarchical framework to estimate the occupancy probability of a species at a site while explicitly accounting for imperfect detection (MacKenzie et al., 2002). Occupancy models provide the means to produce robust inferences into large-carnivore habitat use and ecology on very large scales relevant to their management and conservation (Chanchani et al., 2016).

In Nepal, limited research has focused on estimating leopard (*Panthera pardus fusca*) occupancy and its drivers, while studies that have been conducted are site specific and do not assess landscape scale occupancy (Sigdel et al., 2025). Most previous studies have been conducted within protected areas (Thapa et al., 2014; Carter et al., 2015 Kandel et al., 2020; Thapa et al., 2021), despite the majority of viable leopard habitat in Nepal occurring outside these protected areas (Jnawali et al., 2011). The objectives of our study are to (a) estimate leopard occupancy outside of protected areas, and (b) identify environmental (forest cover, mosaic, wild prey, terrain ruggedness) and anthropogenic (dogs, livestock) determinants of leopard occupancy in a multi-use landscape in Nepal. By quantifying leopard occupancy across a gradient of human influence extending from the peripheries of protected areas into intensively used landscapes, we establish a baseline for understanding large carnivore persistence in human-modified systems and contribute to broader insights into carnivore conservation in multi-use environments globally.

2. Methods

2.1. Study area and design

We conducted the study in an approximately 32,057 km^2 region in central Nepal, known as the Chitwan-Annapurna Landscape (CHAL, Fig. 1). This landscape extends from the southern lowlands (Terai) to the Himalayan Mountain Range (Ministry of Forest and Soil Conservation, 2015).

Our sampling area consisted of a survey grid (~7105 km^2, Fig. 1) that lies within the larger CHAL and is a multi-use forested landscape including lowland plains and steep-sided hills (altitude 200 m - 4000 m) that lies between two protected areas i.e., Chitwan National Park (CNP) in the south and Annapurna Conservation Area (ACA) in the north. We divided the study area into 145, 7 × 7 km grid cells (Fig. 1) to approximate the average home range size of leopards in Nepal (17 and 48 km^2, for females and males respectively, Odden and Wegge, 2005). In each grid cell (hereafter "sites"), we surveyed 9 km of transects, divided into 200-meter sections. Each 200 m section was considered a spatial replicate in which leopard and other wildlife signs were recorded. Leopard habitat use is highly variable at fine spatial scales, with individuals commonly using specific microhabitats such as ridge lines for resting, scent-marking, and travel (*personal field observations*). Thus, the 200 m scale was considered reasonable to reflect variation in sign deposition across microhabitat types, which coarser sampling intervals (e.g., ≥500 m) would likely obscure. Transects were conducted along trails and potential routes that carnivores such as leopards use. The 9 km survey length was comparable with the survey lengths used in the tiger (*Panthera tigris*) monitoring protocol described by the Government of Nepal (DNPWC, 2017). Thus, our detection matrix consisted of a total of 45 200-m spatial replicates for each of the 145 grids, except in some grids ($n = 13$) where a complete length of 9 km was not feasible due to logistical constraints such as inaccessible terrain. Although 13 grids were not fully accessible due to terrain constraints, they were retained in the analysis; survey effort within grids ranged from a minimum of 4 km to a maximum of 9 km. Sampling was conducted proportional to the land use composition within each grid cell (Barber-Meyer et al., 2013; Thapa et al., 2021). For example, if a site consisted of 50% forest and 50% agricultural field, we surveyed 4.5 km in each category which allowed us to produce a representative sample of each grid, and thus the landscape.

2.2. Field Survey

We conducted field surveys in the spring of 2021 (10 February- 31 March), prior to the start of the monsoon season, to minimize the effect of heavy and consistent rain that could wash away wildlife signs. The research was conducted under permit number 2077/78/824 from the Department of Forest and Soil Conservation, Government of Nepal. The field survey was conducted by a team of 12 field surveyors, divided into 4 groups, with 3 surveyors in each group. In each grid cell, surveyors recorded signs of leopard (scat, tracks, scrape and scratch marks), wild prey (tracks, pellet droppings), livestock (hoof marks, dung), and free ranging dogs (tracks, scat, direct observation). To minimize false positives due to misidentification of wildlife signs, surveyors were instructed only to record signs identified with high confidence (following a field guide developed by Jhala et al. (2021)). Although tigers (the most likely species to be confused with leopards) were not detected in any of our study grids during large-scale camera trapping efforts (*personal observation*), we still made efforts to avoid potential confusion between tiger and leopard signs. We adopted a protocol based on the morphological characteristics of signs between leopards and tigers as explained in the field protocol by Singh LAK (2000). Leopard pugmarks are smaller: front foot width ($\sim$mean 8–9 cm for leopard, 12.5–14.2 cm for tiger); pad size width ($<$6.5 cm for leopard, 8.8–10 cm for tiger), adult stride length ($\sim$mean 90 cm in leopard, $>$ 100 cm in tiger), scrapes ($<$25 cm long and $<$15 cm wide for leopard, $>$ 35 cm long and $>$19 cm wide for tiger), and scats (2–4 cm for leopard, $>$ 11 cm in diameter at widest part of the scat for tiger) (McDougal, 1999; Singh et al., 2014; Rostro-García et al., 2018; Lamichhane et al., 2021). Tiger scats are also usually less coiled than leopard scats with longer distances between successive narrowing coils (Wang and Macdonald, 2009).

2.3. Covariates for leopard occupancy and detection probability

We used field surveys and remotely sensed data to derive a range of covariates for modeling detection probability and occupancy of leopards (Table 1). To explain variation in detection probability, we considered two survey covariates: livestock presence and track type (forest tracks, dirt roads, farmland trails). Livestock grazing (cattle and goat flocks) is widespread across the altitudinal gradient of Nepal's hill region (Thapa et al., 2016). During livestock herding/grazing people often use established farmland trails, dirt roads, and forest tracks which might obscure wildlife signs (including leopards) through trampling. Thus, we hypothesized that the detection of livestock presence may negatively impact the ability to detect leopard signs. We also hypothesized that leopard detection probability may be higher on tracks within forests as compared to farmland trails and dirt roads as they are comparatively less used/disturbed by vehicles, making signs available for a longer period to be detected. We also hypothesized that detection would be higher in trails within farmlands than dirt roads as farmland trails are primarily for people to travel and will have less disturbance compared to dirt roads which are used by vehicles.

We used literature to identify and select covariates that we *a priori* hypothesized were important to explain heterogeneity in leopard occupancy. Leopards use a variety of land cover types but extensively use forest areas that are interspersed in human-dominated landscapes as habitat refugia (Harihar et al., 2011; Gubbi et al., 2020; Thapa et al., 2021). Leopards are also adept in using other land use categories such as tea estates (Kshettry et al.,2017), farmlands (Athreya et al., 2013, 2015), and peri-urban areas (Bista et al., 2022). Our study area is characterized by a mosaic of farmlands which could potentially supplement the available natural habitat for leopards. Thus, we hypothesized that forested areas (deciduous, or mixed forest with tree height $>$ 2 m and $>$ 60% tree cover) and mosaics (patches covered by small-scale cultivation with $\geq$40% natural vegetation or tree cover) would be positively associated with leopard occupancy. We used freely available land cover data (30-meter resolution) from MODIS (ORNL DAAC, 2018. MODIS and VIIRS Land Products Global Subsetting and Visualization Tool. ORNL DAAC, Oak Ridge, Tennessee, USA). We hypothesized that terrain ruggedness would be positively associated with leopard occupancy, as leopards are ambush hunters and exploit rocky escarpments for cover to launch attacks on their prey species (Sari et al., 2020). In the Churia hills of Nepal, the ruggedness of the landscape has also been found to positively influence leopard occupancy (Lamichhane et al., 2021) while in India leopard occupancy has been positively affected by the presence of rocky escarpments and boulders (Athreya et al., 2015). We used the terrain ruggedness index developed by Riley and Degloria (1999).

The distribution of predators is often positively influenced by the distribution of their primary prey species (Palomares et al., 2001; Spong, 2002; Broomhall et al., 2003). Among the large carnivores in the genus *Panthera*, leopards have the broadest dietary niche and are known to prefer medium-sized prey (mean body weight $<$ 25 kg) (Hayward et al., 2006). In Nepal and other similar ecological regions of South Asia, leopard diet consists of both wild and domestic prey (livestock and dogs, Aryal et al., 2009; Shehzad et al., 2015;

Table 1
Covariates affecting leopard (*Panthera pardus fusca*) detection (p) and occupancy (ψ) in the Chitwan-Annapurna Landscape, Nepal. The "+ " and "-" signs indicate the *a priori* predictions regarding the hypothesized direction of the effect. "Na" is Not Applicable.

Covariate	Type	Description	Value range minimum-maximum (average)	*A priori relationship*	
				p	*psi* (*ψ*)
Forest	Continuous	Percentage of the survey grid covered by forest (evergreen, deciduous, or mixed forest) with tree height $>$ 2 m and 60% tree cover.	4.89–78.75 (36.39)	Na	+
Mosaic	Continuous	Percentage of the survey grid covered by small-scale cultivation with greater than or equal to 40% of natural vegetation or tree cover.	0–17.33 (1.46)	Na	+
Topographic Ruggedness Index (TRI)	Continuous	The average terrain ruggedness index of each grid was calculated using an SRTM digital elevation model (30 m; Riley and Degloria, 1999). Lower values represent flat surfaces, higher values represent rugged surfaces	4.70–54.71 (33.18)	Na	+
Wild Prey	Continuous	The probability of site use (occupancy) of medium-sized prey (chital, red muntjac, rhesus macaques, wild boar) in each grid.	0.24–0.96 (0.66)	Na	+
Dogs	Continuous	The proportion of the number of replicates (200 m) with signs of dogs (direct obs., scats, and marks) to the total number of surveyed replicates in each grid.	0–0.61 (0.17)	Na	+
Livestock	Continuous	The proportion of the number of replicates (200 m) with livestock (cattle, goat, buffalo) signs (direct obs., dung, hoof marks) to the total number of surveyed replicates in each grid.	0–1 (0.49)	Na	+
Livestock	Categorical	Detection/non-detection of livestock signs (direct observation, dung, hoof marks) in each survey replicate (200 m) in each grid.	0,1	-	Na
Track type	Categorical	Three different segment types - forest tracks (0), dirt roads (1), and farmland trails (2) surveyed in each grid.	0,1,2	+ /-	Na

Kshettry et al., 2018; Kandel et al., 2020). Leopards also hunt rhesus macaques (*Macaca mulatta*) and other primates where available (Puri et al., 2020). Our study system is diverse in terms of wild prey availability for leopards with the presence of medium-sized ungulates such as chital (*Axis axis*), red muntjac (locally refered to as barking deer) (*Muntiacus muntjak*), wild boar (*Sus scrofa*), and rhesus macaques (Ministry of Forest and Soil Conservation , 2015). Leopards also predate on livestock and feral species, this is thought to occur when the availability of wild prey is low (Athreya et al., 2014; Shehzad et al., 2015). Local livelihood within our landscape is heavily reliant on income from livestock husbandry, particularly goats, which in terms of body weight and size are like the prey preferred by leopards. The ubiquitous presence of free ranging dogs in our study region, which leopards are known to predate (Athreya et al., 2014), further expands the prey base for leopards in our study system.

To quantify spatial variation in wild prey availability, we estimated site-use probability (ψ) for key prey species (chital, red muntjac, wild boar, and rhesus macaques) using an occupancy modeling framework that accounts for imperfect detection (see Supplementary Table S1 for full model results). Across the study area, wild prey site-use probability was relatively high but spatially heterogeneous, with values ranging from 0.24 to 0.96 (mean = 0.66), indicating substantial variation in prey use among sites. We interpret prey site-use probability as a detection-corrected proxy for spatial variation in prey availability, reflecting the likelihood that prey species used a site during the sampling period. In contrast, occupancy models for domestic species (livestock and dogs) were not estimable due to near-ubiquitous presence across sites. Therefore, we used a Relative Abundance Index (RAI), defined as the proportion of sampled segments with signs, as a proxy for their relative availability (Puri et al., 2020; Thapa et al., 2021. RAI values for livestock and dogs also showed variation across sites (Table 1) but represent relative sign frequency rather than detection-corrected site use. Wild prey site-use probability was subsequently used as a covariate in leopard occupancy models.

2.4. Data analysis

We employed an occupancy modeling framework (MacKenzie et al., 2002) to estimate leopard occurrence. Given the large home ranges of leopards relative to grid cell size, we interpret the estimated occupancy probability (ψ) as probability of site use (Mackenzie & Royle, 2005). Accordingly, hereafter occupancy is used to refer to the probability that a site was used during the sampling period, rather than being continuously occupied. We used the Hines et al. (2010) occupancy model that explicitly considers spatial autocorrelation in detections along the 200 m segments of transects within each site, and accounts for the spatial dependence between detections (Thapa et al., 2021; Lamichhane et al., 2021; Paudel et al., 2022). The Hines et al. model tests for dependence in sign detection through a spatial dependence parameter, θ. We used Akaike information criteria (AIC) based model ranking and a two-stage model fitting procedure (Karanth et al., 2011), in which first we used the AIC value-based ranking to find the best-fit model for detection probability while keeping the occupancy parameter constant (i.e., ψ (.)) (Morin et al., 2020). In the subsequent stage, we fixed the top-ranked detection model (i.e., p(top)) and considered *a priori*-defined ecologically meaningful combinations of our hypothesized covariates (n = 19, Table 2) to explain variation in leopard site use probability. To prevent variable-selection ambivalence resulting from using 95% confidence intervals with an information theoretic approach, we used 85% confidence intervals while considering our parameter estimates (Arnold, 2010; Sutherland et al., 2023). All covariates were assessed for multicollinearity (Pearson's correlation coefficient and variance inflation factor (VIF), Supplementary Information, Figure S1). Wild prey availability

Table 2
Ecologically meaningful combinations (n = 19) of predictors used in the occupancy model to explain leopard (*Panthera pardus fusca*) occupancy in the Chitwan-Annapurna Landscape (CHAL), Nepal.

Covariate combinations	
Habitat models	
1	Forest
2	Mosaic
3	Forest and mosaic
Prey models	
4	Wild prey
5	Dog
6	Livestock
7	Wild prey and dog
8	Wild prey and livestock
9	Dog and livestock
10	Prey, dog, and livestock
Habitat and prey combination models	
11	Forest and wild prey
12	Mosaic and wild prey
13	Forest and dog
14	Mosaic and dog
15	Mosaic and livestock
16	Mosaic, prey, and dog
17	Mosaic, prey, and livestock
18	Forest, dog, and livestock
19	Mosaic, dog, and livestock

and TRI were found to be highly correlated (i.e., $r \geq |0.70|$), and thus TRI was dropped from the analysis. No other evidence of collinearity was found. All covariates used in modeling were scaled and centered to have a mean of zero and unit variance. We explored model fit and overdispersion using goodness of fit tests (MacKenzie and Bailey, 2004) on the global model to a subset ($n = 7$ replicates) of our data (Bayandonoi et al., 2021). The dataset was reduced as the number of replicate surveys varied and the goodness of fit estimation procedure can produce unreliable results in such circumstances (MacKenzie et al., 2017). We found no evidence for lack of fit and overdispersion ($p = 0.27$, $\hat{c}=0.75$) in our goodness of fit test. The occupancy analysis and model ranking were conducted in R version 4.2.1 (R Core Team, 2021) using package *RPresence* (MacKenzie and Hines, 2023) and its associated functions.

3. Results

We surveyed 1277 km of transects and recorded leopard signs in 69 of 145 grids, recording 226 leopard signs (pugmarks=154, scats=72) which resulted in a naïve occupancy of 0.48 i.e., before accounting for heterogeneity in the detection process. Based on AIC values, the spatial autocorrelation model (Hines et al., 2010) was more parsimonious than the standard single-season model (MacKenzie et al., 2002) [Supplementary Information Table S2]. This confirmed our *a priori* expectation of a lack of independence in the detection of leopard signs across the spatial replicates. Detection of leopard signs on our survey transects was spatially correlated ($\theta^0 = -3.40$, 85% CI = −3.68- −3.12; $\theta^1 = 4.03$, 85% CI = 3.47–4.59), where θ^0 denotes the probability that a species is available in a survey segment given that it was not available in the previous segment; and θ^1 denotes the probability that a species is available in a transect segment given that it was available in the previous segment.

The top model for detection probability [Table 3] indicated that the detection of leopard signs was positively influenced by livestock presence [$\beta_{lvstk} = 0.91$, 85% CI = 0.17–1.66] and forest tracks [$\beta_{fr} = 0.71$, 85% CI = 0.07–1.35]. Detection probability was negatively influenced by vehicle roads [$\beta_{dr} = -1.76$, 85% CI = -2.77 - −0.75] and farm field tracks [$\beta_{ar} = -2.54$, 85% CI = -3.58 - −1.50]. The mean detection probability of leopard signs from the top-ranked detection model was $p = 0.55$ (85% CI = 0.39–0.69). Fig. 2 shows values of leopard sign detection probability in different track types with and without livestock presence.

At the scale of the study grids, model selection results with the top detection parameter fixed [Table 4], show that leopard occupancy was positively associated with wild prey occupancy ($\beta_{prey} = 0.75$, 85% CI = 0. 15–1.35) (Fig. 3). The landscape-scale predictions of how wild prey site use probability affects leopard occupancy across the landscape are presented in Fig. 4. The top model predicted a mean occupancy probability by leopards of $\psi = 0.73$ (85% CI = 0. 52–0.86).

The model selection results for prey site use clearly indicate that cropland is an important predictor of site-use probability (ψ) for leopard prey species. The top-ranked model includes cropland as the sole covariate on occupancy. The positive coefficient for cropland ($\beta = 1.71$, 85% CI: 0.07–3.35) suggests that prey species are more likely to use sites with higher cropland cover. Although the confidence interval is relatively wide, it does not overlap zero, indicating a moderately strong positive effect.

4. Discussion

Our study offers compelling evidence that the distribution of large carnivores, such as leopards, is positively influenced by the presence of wild prey. In the Chitwan Annapurna Landscape of Nepal, leopards are more likely to occupy areas utilized by their native wild prey such as red muntjac, rhesus macaques, chital, and wild boars. This emphasizes the critical importance of conserving native wild prey species to ensure the long-term persistence of leopards outside of conservation areas and national parks. Our study evaluated *a priori* hypotheses regarding the influence of habitat structure, prey availability, and anthropogenic factors on leopard occupancy in a multi-use landscape. Of these, only the presence of wild prey was supported, whereas habitat and anthropogenic covariates were not retained in top models. Interpreting these results in the context of prior expectations provides important insight into the ecological processes shaping leopard distribution and their implications for conservation outside protected areas.

Consistent with our *a priori* prediction, leopard occupancy was positively associated with wild prey occurrence. This finding aligns with a broad body of work demonstrating the role of prey species in determining the distribution of large carnivores in several big cat species, including tigers (Thapa et al., 2016, Duangchatrasiri et al., 2019), lions (Everatt et al., 2019), snow leopards, and jaguars (Rabelo et al., 2019). In our study landscape, which extends beyond protected areas, leopards exhibited higher occupancy in regions with a greater presence of their native wild prey. Furthermore, the occupancy of these prey species was positively associated with agricultural lands. The use of agricultural lands by ungulates to avoid predation is well documented (Krishna et al., 2016; Khara et al.,

Table 3
Model selection results for survey covariates influencing the detection probability of leopard signs in the Chitwan-Annapurna Landscape, Nepal. p is the detection probability of leopard (*Panthera pardus fusca*) signs, K is the number of model parameters, −2logL is the logarithm of the negative likelihood function; AIC is Akaike's information criterion used for model ranking, ΔAIC is the difference in AIC value between the top model and other models in the set and ωAIC is the relative likelihood of the model in the set. Occupancy, theta, and theta prime were kept constant across all models and thus are not shown.

Model	K	−2logL	AIC	ΔAIC	ωAIC
p (~trail type + livestock)	7	1454.13	2894.26	0	0.77
p (~trail type)	6	1458.67	2905.34	2.54	0.23
p (.)	4	1469.50	2931.00	9.37	0.00
p (~livestock)	5	1469.27	2928.54	11.14	0.00

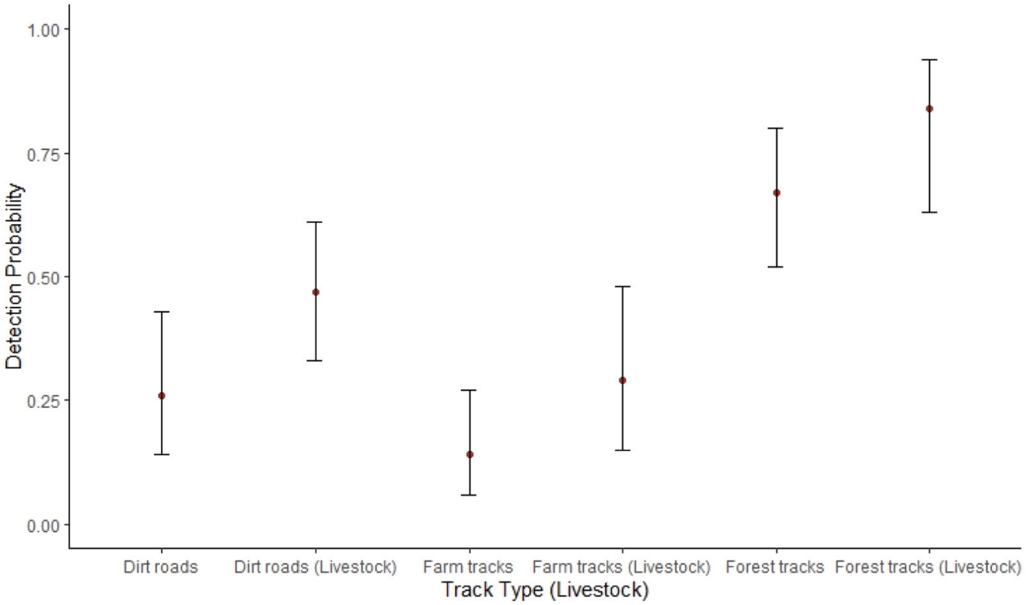

Fig. 2. Detection probability (with 85% CI) of leopard (*Panthera pardus fusca*) signs along the survey transects in different transect types (dirt roads, farm tracks, forest tracks) with and without livestock presence.

Table 4
Model selection results for landscape covariates influencing the probability of leopard (*Panthera pardus fusca*) occupancy across 145 sample sites surveyed in the Chitwan-Annapurna Landscape, Nepal. Models with uninformative parameters are not shown (see supplementary information Table S3 for full model ranking). ψ = probability of occupancy of leopards at the grid cell level; *K* is the number of model parameters, −2logL is the logarithm of the negative likelihood function; AIC is Akaike's information criterion used for model ranking, ΔAIC is the difference in AIC value between the top model and other model and ωAIC is the relative likelihood of the model. The top detection model (From Table 3: top detection covariates i.e., *p* (trail type + livestock), theta, and theta prime were held constant for all models.

Model	K	−2logL	AIC	ΔAIC	ωAIC
ψ (~prey)	8	1448.89	1464.89	0	0.84
ψ (.)	7	1454.12	1468.12	3.23	0.16

2021; Tizanni et al., 2022; Blum et al., 2023;), and the increasing incidents of crop depredation by ungulates in our study area (Bist and Song., 2021; Baral et al., 2021) might suggest that these fields offer accessible, high-nutrient forage (Mekonen S., 2020).

Our findings support the human shield hypothesis, which posits that prey species may use human-dominated landscapes as refuges from predators (Berger J., 2007; Lamichhane et al., 2023). This behavior aligns with the concept of a 'landscape of fear', where prey avoid areas, they perceive as dangerous due to predator activity (Laundre et al., 2010; Epperly et al., 2021). It is likely that leopards are adapting their habitat use in response to their prey species' preferences, using areas where prey is distributed. Optimal foraging theory further supports this observation as predators are known to maximize foraging efficiency by occupying regions where prey species are available (Blame et al., 2020; Everatt et al., 2023; Yadav et al., 2024).

Interspecific competition within the carnivore guild also influences the distribution and feeding strategies of the carnivore community (Ordiz et al., 2020; Prughand Sivy., 2020). Our findings highlight that the absence of a dominant carnivore shapes the habitat selection strategies of a subordinate congener by eliminating the horizontal interaction within the carnivore guild (Smith et al., 2023). There is well-documented evidence of interference competition between leopards and tigers, where leopards adjust their home range to edge habitats to avoid tigers (Odden et al., 2010; Harihar et al., 2011; Steinmetz et al., 2013). Leopards often shift to sub-optimal edge habitats with lower tiger densities and supplement their diet with livestock and free-ranging dogs (Harihar et al., 2011; Bhattarai & Kindlmann, 2012; Pokheral and Wegge., 2019; Lamichhane et al., 2019). The absence of tigers in our study system releases leopards from the constraints of competitive interactions, which allows them to more freely exploit available prey (Carter et al., 2015).

As leopards follow their prey to agricultural fields, the likelihood of human encounters increases, a trend already observed in rising leopard attacks in such areas (Baral et al., 2021; Poudel et al., 2023). Leopards also rely on livestock as a significant (~1/3) part of their diet (Athreya et al., 2014; Kshettry et al., 2018; Dhungana et al., 2019; Kandel et al., 2020; Lamichhane et al., 2023), which further complicates human-wildlife interactions. Thus, given the prey availability in agricultural lands and the potential of prey switching by leopards towards livestock (Shehzad et al., 2015), efforts to manipulate the foraging behavior of wild prey species from agricultural fields is an important consideration for livestock and human safety. Manipulation may involve promoting less palatable crop varieties to deter wild ungulates (Widen et al., 2023), and providing subsidies or buyback guarantees for these crops (Badola et al., 2021).

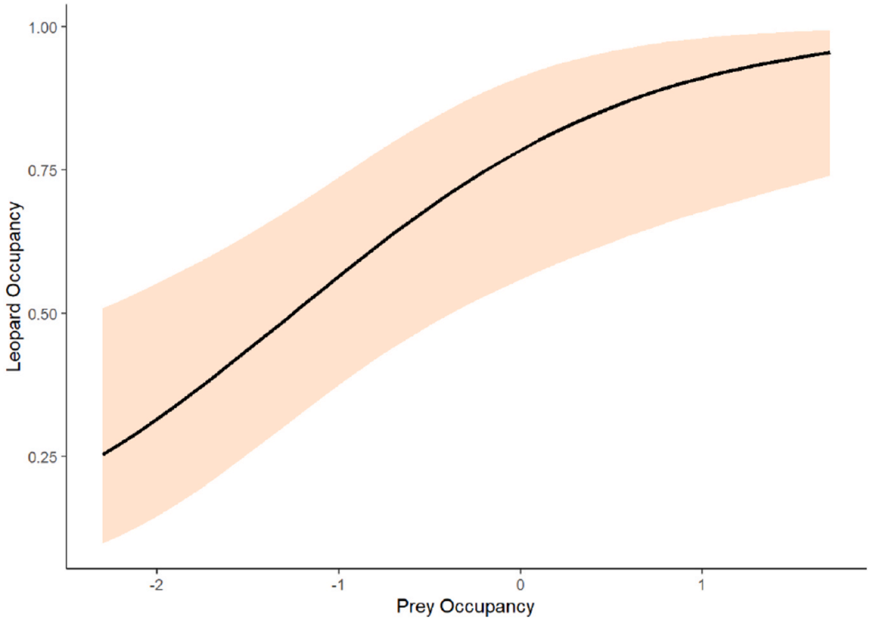

Fig. 3. Marginal estimates of leopard (*Panthera pardus fusca*) occupancy as a function of wild prey site use with 85% confidence intervals (shaded region) from the top model. Wild prey species include rhesus macaques (*Macaca mulatta*), wild boar (*Sus scrofa*), red muntjac (*Muntiacus muntjak*), and chital (*Axis axis*).

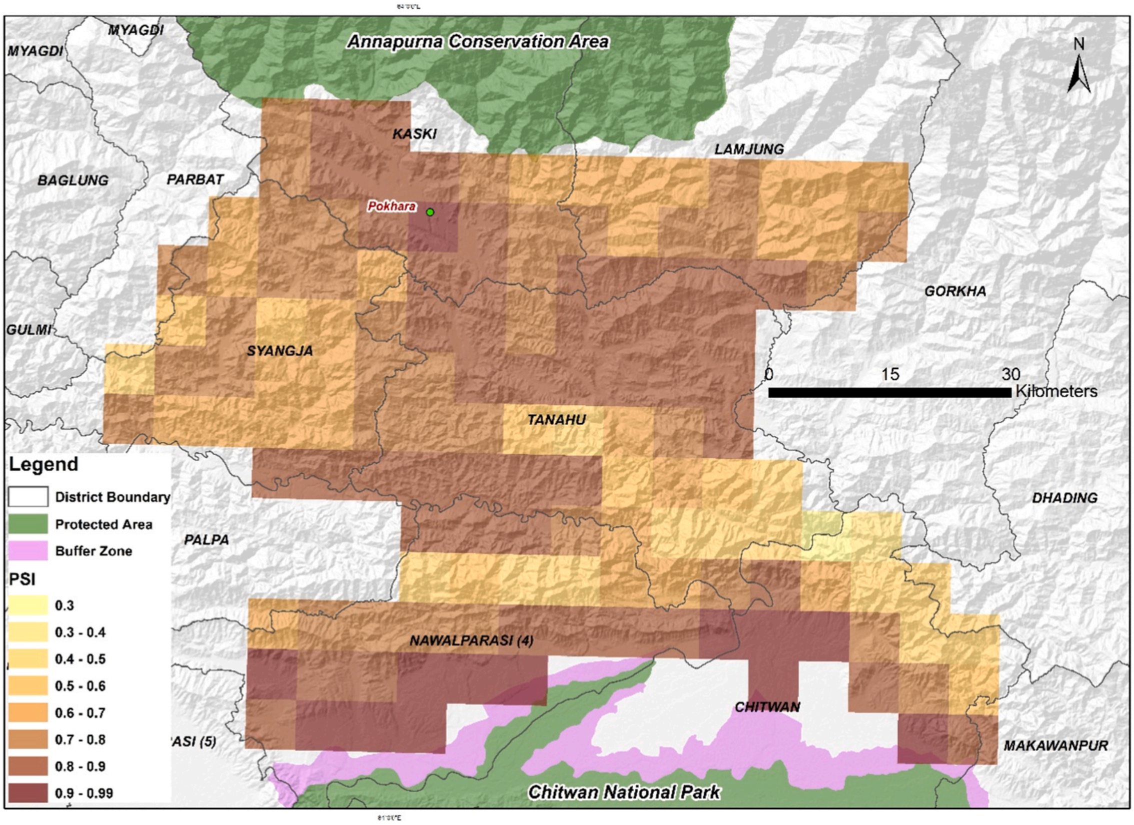

Fig. 4. Probability of leopard *(Panthera pardus fusca)* occupancy (ψ) across the 7105 km^2 region in the Chitwan Annapurna Landscape (CHAL), Nepal.

Educating local communities about leopard behavior and prey dynamics can also help reduce conflicts by enabling residents to implement preventive measures, reducing the need for lethal control.

Effective conservation of large carnivores like leopards requires expansive, connected habitats (Crooks et al., 2011), but increasing human populations are creating significant land-use conflicts (Di Minin et al., 2016). This demand for land has led to significant habitat degradation and fragmentation, resulting in global range contractions of large carnivores (Wolf and Ripple, 2017). While protected areas are essential for biodiversity conservation (Karanth and Chellam, 2009; Terraube et al., 2020.), there is a growing consensus that they are insufficient for sustaining viable populations of wide-ranging large carnivores in the long term (Ripple et al., 2014; Choki et al., 2023). Climate change further complicates conservation efforts by altering species distributions including wild ungulates (Zhang et al., 2022; Bhasin et al., 2024; Malpeli et al., 2024). Leopards are also affected by the changing climate in Nepal, and future conservation strategies might benefit from accounting for climate impacts while devising conservation strategies for leopards (Baral et al., 2023). Therefore, transitioning from a traditional protected area-centric approach to also include habitat patches outside of protected areas is crucial for the effective conservation of both carnivores and prey species in Nepal. Such conservation efforts will be most effective if they include community engagement, habitat improvement, and conflict mitigation measures to ensure the safety of local communities (Lamichhane et al., 2019). Implementing area based conservation measures such as Other Effective Area-Based Conservation Measures (OECMs) could provide some legal protection for leopards and their habitats while allowing sustainable and pro-conservation land use planning (Chen et al., 2024; Dudley et al., 2018). OECMs are areas outside established protected areas that ensure positive and sustainable biodiversity conservation outcomes (Jonas et al., 2024). Although no OECMs are currently designated in Nepal, community forests in Nepal's hill region could serve as potential OECMs, with leopards acting as indicators of ecosystem health. Such novel conservation measures can offer better legal protection for leopards, prey, and habitat while allowing sustainable local use of conserved areas.

We hypothesized that forest cover, mosaic habitats, and terrain ruggedness would positively influence leopard occupancy. However, these variables were not retained in top models. There are some non-mutually exclusive explanations for this result. First, habitat effects may be mediated indirectly through prey distribution. In many systems, habitat structure influences carnivore occurrence primarily by structuring prey availability (Palomares et al., 2001), which may explain why prey emerged as an important driver of leopard occupancy. Indeed, terrain ruggedness was correlated with prey and removed from the analysis, suggesting that its ecological effect may already be captured through prey distribution. Secondly, this result is consistent with evidence that leopards are highly adaptable habitat generalists capable of using forests, agricultural mosaics, and peri-urban environments (Kshettry et al., 2017; Athreya et al., 2015; Bista et al., 2022). In such systems, prey availability may override habitat constraints, leading to weak or inconsistent habitat relationships.

Our study demonstrates that sign-based surveys of carnivores when properly combined with occupancy models, can establish baseline estimates for tracking changes across large landscapes. As landscapes transform due to factors like urbanization, agriculture, and climate change, monitoring carnivores' adaptability becomes crucial for their long-term persistence (Wolf and Ripple, 2018 DeMars & Boutin., 2018; Takinami et al., 2021). Sign surveys are cost-effective and can cover extensive areas, providing continuous data over time, which can complement more expensive methods such as camera trapping or genetics (McHenry et al., 2016) which provide true occupancy or population density estimates at finer scales (Blanc et al., 2014). By combining these approaches, wildlife managers can develop management plans that address both ecological dynamics and socio-economic shifts, ensuring the long-term conservation of leopards and their prey in Nepal. Monitoring changes in prey abundance and site use over time can provide valuable insights into leopard distribution, informing targeted conservation interventions and context-specific strategies for reducing human-leopard conflicts. Conserving large carnivores within multiple-use forested landscapes requires balancing human safety, livestock protection, and conservation benefits (Bista et al., 2022). Evidence-based site-specific management strategies would help conserve both leopards and wild prey species in Nepal's non-protected areas. Our study underscores the global need to incorporate multi-use landscapes into carnivore conservation planning.

Author contributions

SP, AKF, RCS, MG conceived the study; SP administered the field work and collected the data; SP, AKF, and JPT analyzed the data, AKF, RCS, and MG validated the findings, SP wrote the first draft, and all authors reviewed and edited the paper.

Funding

The authors would like to thank Cornell Atkinson Center for Sustainability for funding this study and the Wildlife Conservation Network for a supplemental grant to support SP through the Pat J. Miller Graduate Scholarship.

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.

Acknowledgements

SP would like to thank Drs Kanchan Thapa and Gokarna Jung Thapa at the World Wildlife Fund Nepal Program for their support during the preparation of the manuscript and Ms. Madhuri Karki at Department of Forest and Soil Conservation (DoFSC) for her support during the permit application process. SP would also like to thank Koustubh Sharma and Asish Bista for their constructive discussions, and all field technicians for their support during data collection. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2026.e04240.

Data availability

Data have limited availability owing to sensitivity concerns of a vulnerable species. Contact Dr. Shashank Poudel at World Wildlife Fund, Nepal for more information.

References

Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's information criterion. J. Wildl. Manag. 74 (6), 1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x.

Aryal, A., Brunton, D., Raubenheimer, D., 2009. Diet and nutrient balancing in leopards (Panthera pardus) in Nepal. Mamm. Biol. 74 (3), 247–252.

Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J., Karanth, K.U., 2014. A cat among the dogs: Leopard Panthera pardus diet in a human-dominated landscape in western Maharashtra, India. Oryx 50 (1), 156–162. https://doi.org/10.1017/S0030605314000106.

Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J., Karanth, K.U., 2015. Spotted in the news: Using media reports to examine leopard distribution, depredation, and management practices outside protected areas in southern India. PLOS One 10 (11), e0142647. https://doi.org/10.1371/journal.pone.0142647.

Badola, R., Ahmed, T., Gill, A.K., et al., 2021. An incentive-based mitigation strategy to encourage coexistence of large mammals and humans along the foothills of Indian Western Himalayas. Sci. Rep. 11, 5235. https://doi.org/10.1038/s41598-021-84119-7.

Baral, K., Adhikari, B., Bhandari, S., Kunwar, R.M., Sharma, H.P., 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 (1). https://doi.org/10.1016/j.heliyon.2022.e12801.

Baral, K., Sharma, H.P., Rimal, B., Thapa-Magar, K., Bhattarai, R., Kunwar, R.M., 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. https://doi.org/10.1371/journal.pone.0260307.

Barber-Meyer, S.M., Jnawali, S.R., Karki, J.B., Khanal, P., Lohani, S., Long, B., MacKenzie, D.I., Pandav, B., Pradhan, N.M.B., Shrestha, R., Subedi, N., Thapa, G., Thapa, K., Wikramanayake, E., 2013. Influence of prey depletion and human disturbance on tiger occupancy in Nepal. J. Zool. 289 (1), 10–18.

Bayandonoi, G., Sharma, K., Alexander, J.S., Lkhagvajav, P., Durbach, I., Buyanaa, C., Munkhtsog, B., Ochirjav, M., Erdenebaatar, S., Batkhuyag, B., Battulga, N., Byambasuren, C., Uudus, B., Setev, S., Davaa, L., Agchbayar, K.-E., Galsandorj, N., MacKenzie, D., 2021. Mapping the ghost: Estimating probabilistic snow leopard distribution across Mongolia. Divers. Distrib. 27 (12), 2441–2453. https://doi.org/10.1111/ddi.13412.

Berger, J., 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biol. Lett. 3 (6), 620–623. https://doi.org/10.1098/rsbl.2007.0415.

Bhasin, A., Ghosal, S., Raina, P., Hore, U., 2024. Climate change impacts on high altitude wildlife distribution: Predicting range shifts for four ungulates in Changthang, eastern Ladakh. Ecol. Front. 44 (2), 365–380.

Bhattarai, B.P., Kindlmann, P., 2012. Habitat heterogeneity as the key determinant of the abundance and habitat preference of prey species of tiger in the Chitwan National Park, Nepal. Acta Theriol. 57 (1), 89–97. https://doi.org/10.1007/s13364-011-0047-8.

Bist, R., Song, C., 2021. Human-wildlife conflict in the community forestry landscape: A case study from two Middle Hill districts of Nepal. Hum. Dimens. Wildl. 27 (6), 554–570. https://doi.org/10.1080/10871209.2021.1980158.

Bista, A., Chanchani, P., Subedi, N., Bajracharya, S.B., 2022. The peri-urban leopards of Kathmandu: Assessing determinants of presence and predation on domestic animals. Oryx 56 (5), 1–10. https://doi.org/10.1017/S0030605320000423.

Blame, G.A., le Roex, N., Rogan, M.S., Hunter, L.T.B., 2020. Ecological opportunity drives individual dietary specialization in leopards. J. Anim. Ecol. 89 (3), 589–600. https://doi.org/10.1111/1365-2656.13109.

Blanc, L., Marboutin, E., Gatti, S., Zimmermann, F., Gimenez, O., 2014. Improving abundance estimation by combining capture–recapture and occupancy data: Example with a large carnivore. J. Appl. Ecol. 51 (6), 1733–1739.

Blum, M.E., Stewart, K.M., Shoemaker, K.T., et al., 2023. Changes in selection of resources with reproductive state in a montane ungulate. Mov. Ecol. 11, 20. https://doi.org/10.1186/s40462-023-00378-1.

Braczkowski, A.R., O'Bryan, C.J., Stringer, M.J., Watson, J.E.M., Possingham, H.P., Beyer, H.L., 2018. Leopards provide public health benefits in Mumbai, India. Front. Ecol. Environ. 16 (3), 176–182. https://doi.org/10.1002/fee.1776.

Broomhall, L.S., Mills, M.G.L., du Toit, J.T., 2003. Home range and habitat use by cheetahs (Acinonyx jubatus) in the Kruger National Park. J. Zool. 261 (2), 119–128.

Carbone, C., Mace, G.M., Roberts, S.C., Macdonald, D.W., 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402 (6759), 286–288.

Carter, N., Jasny, M., Gurung, B., Liu, J., 2015. Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. Glob. Ecol. Conserv. 3, 149–162.

Carter, N.H., Linnell, J.D.C., 2023. Building a resilient coexistence with wildlife in a more crowded world. PNAS Nexus 2 (3), pgad030. https://doi.org/10.1093/pnasnexus/pgad030.

Chanchani, P., Noon, B.R., Bailey, L.L., Warrier, R.A., 2016. Conserving tigers in working landscapes. Conserv. Biol. 30 (3), 649–660.

Chapron, Kaczensky, G., Linnell, P., von Arx, J.D.C., Huber, M., Andrén, D., López-Bao, H., V, J., et al., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346 (6216), 1517–1519. https://doi.org/10.1126/science.1257553.

Chen, X., Tian, T., Pan, H., Jin, Y., Zhang, X., Yang, B., Zhang, L., 2024. Establishing a protected area network in Xinlong with other effective area-based conservation measures. Conserv. Biol., e14297

Choki, K., Dhendup, P., Tenzin, J., Dorji, D., Tenzin, K., Wangmo, T., Penjor, U., 2023. Conservation potential of non-protected area for sympatric carnivores in Bhutan. Glob. Ecol. Conserv. 42, e02395.

Crooks, K.R., Burdett, C.L., Theobald, D.M., Rondinini, C., Boitani, L., 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philos. Trans. R. Soc. B Biol. Sci. 1578, 366.

DeMars, C.A., Boutin, S., 2018. Nowhere to hide: Effects of linear features on predator–prey dynamics in a large mammal system. J. Anim. Ecol. 87 (1), 274–284.

Dhungana, R., Lamichhane, B.R., Savini, T., Dhakal, M., Poudel, B.S., Karki, J.B., 2019. Livestock depredation by leopards around Chitwan National Park, Nepal. Mamm. Biol. 96, 7–13. https://doi.org/10.1016/j.mambio.2019.03.006.

Di Minin, E., Slotow, R., Hunter, L.T., Montesino Pouzols, F., Toivonen, T., Verburg, P.H., et al., 2016. Global priorities for national carnivore conservation under land use change. Sci. Rep. 6 (1), 23814.

DNPWC (2017). Tiger and prey base monitoring protocol 2017 (Nepal) (Vol. 2017). Government of Nepal, Ministry of Forests and Soil Conservation, Department of National Parks and Wildlife Conservation, Babarmahal, Kathmandu, Nepal.

Duangchatrasiri, S., Jornburom, P., Jinamoy, S., et al., 2019. Impact of prey occupancy and other ecological and anthropogenic factors on tiger distribution in Thailand's western forest complex. Ecol. Evol. 9 (5), 2449–2458. https://doi.org/10.1002/ece3.4845.

Dudley, N., Jonas, H., Nelson, F., Parrish, J., Pyhälä, A., Stolton, S., Watson, J.E., 2018. The essential role of other effective area-based conservation measures in achieving big bold conservation targets. Glob. Ecol. Conserv. 15, e00424.

Epperly, H.K., Clinchy, M., Zanette, L.Y., et al., 2021. Fear of large carnivores is tied to ungulate habitat use: Evidence from a bifactorial experiment. Sci. Rep. 11, 12979. https://doi.org/10.1038/s41598-021-92469-5.

Everatt, K.T., Kokes, R., Robinson, H., Kerley, G.I.H., 2023. Optimal foraging of lions at the human wildlands interface. Afr. J. Ecol. 61 (3), 306–319. https://doi.org/10.1111/aje.13113.

Everatt, K.T., Moore, J.F., Kerley, G.I.H., 2019. Africa's apex predator, the lion, is limited by interference and exploitative competition with humans. Glob. Ecol. Conserv. 20, e00758. https://doi.org/10.1016/j.gecco.2019.e00758.

Fuller, A.K., Augustine, B.C., Morin, D.J., Pigeon, K., Boulanger, J., Lee, D.C., Bisi, F., Garshelis, D.L., 2022. The occupancy–abundance relationship and sampling designs using occupancy to monitor populations of Asian bears. Glob. Ecol. Conserv. https://doi.org/10.1016/j.gecco.2022.e02075.

Gerland, P., Raftery, A.E., Ševčíková, H., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick, B.K., Chunn, J., Lalic, N., Bay, G., Buettner, T., Heilig, G.K., Wilmoth, J., 2014. World population stabilization unlikely this century. Science 346 (6206), 234–237. https://doi.org/10.1126/science.1257469.

Gubbi, S., Sharma, K., Kumara, V., 2020. Every hill has its leopard: Patterns of space use by leopards (Panthera pardus) in a mixed-use landscape in India. PeerJ 8, e10072. https://doi.org/10.7717/peerj.10072.

Habib, B., Ghaskadbi, P., Khan, S., Hussain, Z., Nigam, P., 2021. Not a cakewalk: Insights into movement of large carnivores in human-dominated landscapes in India. Ecol. Evol. 11 (4), 1653–1666. https://doi.org/10.1002/ece3.7156.

Harihar, A., Pandav, B., Goyal, S.P., 2011. Responses of leopard Panthera pardus to the recovery of a tiger Panthera tigris population. J. Appl. Ecol. 48 (3), 806–814.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., Kerley, G.I.H., 2006. Prey preferences of the leopard (Panthera pardus). J. Zool. 270 (2), 298–313. https://doi.org/10.1111/j.1469-7998.2006.00139.x.

Hines, J.E., Nichols, J.D., Royle, J.A., MacKenzie, D.I., Gopalaswamy, A.M., Kumar, N.S., Karanth, K.U., 2010. Tigers on trails: Occupancy modeling for cluster sampling. Ecol. Appl. 20 (5), 1456–1466. https://doi.org/10.1890/09-0321.1.

Holland, O., Stephens, A., Doody, J.S., Sherwen, S., 2018. Risk, behaviour and conservation of large carnivores. In: Getz, In.W.M., Fortmann, L. (Eds.), Large carnivore conservation and management, pp. 1–20.

Hovardas, T., Penteriani, V., Trouwborst, A., López-Bao, J.V., 2021. Conservation and management of large carnivores—Local insights for global challenges. Front. Ecol. Evol. 9, 682444. https://doi.org/10.3389/fevo.2021.682444.

Jacobson, A.P., Gerngross, P., Lemeris, J.R., Schoonover, R.F., Anco, C., Breitenmoser-Würsten, C., Durant, S.M., Farhadinia, M.S., Henschel, P., Kamler, J.F., Laguardia, A., Rostro-García, S., Stein, A.B., Dollar, L., 2016. Leopard (Panthera pardus) status, distribution, and the research efforts across its range. PeerJ 4, e1974. https://doi.org/10.7717/peerj.1974.

Jhala, Y., Gopal, R., Mathur, V., et al., 2021. Recovery of tigers in India: Critical introspection and potential lessons. People Nat. 3 (2), 281–293. https://doi.org/10.1002/pan3.10177.

Jhala, Y.V., Qureshi, Q., & Gopal, R. (2021). Field guide: Monitoring tigers, co-predators, prey and their habitats (5th ed.). National Tiger Conservation Authority & Wildlife Institute of India.

Jnawali, S.R., Baral, H., Lee, S., Acharya, K., Upadhyay, G., Pandey, M., & Griffiths, J. (2011). The status of Nepal mammals: The national red list series. Department of National Parks and Wildlife Conservation.

Jonas, H.D., Wood, P., Woodley, S. (Eds.), 2024. Guidance on other effective area-based conservation measures (OECMs). IUCN WCPA Good Practice Series. No, 36. IUCN.

Kandel, S.R., Lamichhane, B.R., Subedi, N., 2020. Leopard (Panthera pardus) density and diet in a forest corridor of Terai: Implications for conservation and conflict management. Wildl. Res. 47 (5), 460–467. https://doi.org/10.1071/WR19126.

Karanth, K.U., Chellam, R., 2009. Carnivore conservation at the crossroads. Oryx 43 (1), 1–2. https://doi.org/10.1017/S003060530843106X.

Karanth, K.U., Gopalaswamy, A.M., Kumar, N.S., Vaidyanathan, S., Nichols, J.D., MacKenzie, D.I., 2011. Monitoring carnivore populations at the landscape scale: Occupancy modelling of tigers from sign surveys. J. Appl. Ecol. 48 (4), 1048–1056.

Kéry, M., & Royle, J.A. (2015). Applied hierarchical models in ecology: Modelling abundance, occurrence and species richness using R and BUGS (Vol. 1). Academic Press.

Kéry, M., & Royle, J.A. (2020). Applied hierarchical models in ecology: Modelling abundance, occurrence and species richness using R and BUGS (Vol. 2). Academic Press.

Khara, A., Khanyari, M., Ghoshal, A., et al., 2021. The forgotten mountain monarch? Understanding conservation status of the Vulnerable Ladakh urial in India. Eur. J. Wildl. Res. 67, 62. https://doi.org/10.1007/s10344-021-01492-4.

Krishna, Y.C., Kumar, A., Isvaran, K., 2016. Wild ungulate decision-making and the role of tiny refuges in human-dominated landscapes. PLOS ONE 11 (3), e0151748. https://doi.org/10.1371/journal.pone.0151748.

Kshettry, A., Vaidyanathan, S., Athreya, V., 2017. Leopard in a teacup: A study of leopard habitat-use and human-leopard interactions in north-eastern India. PLOS ONE 12 (5), e0177013. https://doi.org/10.1371/journal.pone.0177013.

Kshettry, A., Vaidyanathan, S., Athreya, V., 2018. Diet selection of leopards (Panthera pardus) in a human-use landscape in north-eastern India. Trop. Conserv. Sci. 11, 1–9. https://doi.org/10.1177/1940082918764635.

Lamichhane, S., Lamichhane, B.R., Gurung, A., Rayamajhi, T., Dahal, T.P., Regmi, P.R., Pokheral, C.P., Pathak, A., Panta, G., Kandel, R.C., Oli, M.K., 2023. Non-exploitative human disturbance provides shelter for prey from predator. S. Ecol. Evol. 13, e10200. https://doi.org/10.1002/ece3.10200.

Lamichhane, B.R., Lamichhane, S., Regmi, R., Dhungana, M., Thapa, S.K., Prasai, A., Gurung, A., Bhattarai, S., Paudel, R.P., Subedi, N., 2021. Leopard (Panthera pardus) occupancy in the Chure range of Nepal. Ecol. Evol. 11 (20), 13641–13660. https://doi.org/10.1002/ece3.8105.

Lamichhane, B.R., Lamichhane, S., Regmi, R., Dhungana, M., Thapa, S.K., Prasai, A., Gurung, A., Bhattarai, S., Paudel, R.P., Subedi, N., 2021. Leopard (Panthera pardus) occupancy in the Chure range of Nepal. Ecol. Evol. 11 (20), 13641–13660. https://doi.org/10.1002/ece3.8105.

Lamichhane, B.R., Leirs, H., Persoon, G.A., Subedi, N., Dhakal, M., Oli, B.N., Reynaert, S., Sluydts, V., Pokheral, C.P., Poudyal, L.P., Malla, S., de Iongh, H.H., 2019. Factors associated with co-occurrence of large carnivores in a human-dominated landscape. Biodivers. Conserv. 28, 1473–1491. https://doi.org/10.1007/s10531-019-01737-4.

Lamichhane, B.R., Pokheral, C.P., Poudel, S., et al., 2018. Rapid recovery of tigers Panthera tigris in Parsa Wildlife Reserve, Nepal. Oryx 52 (1), 16–24. https://doi.org/10.1017/S0030605317000886.

Laundré, J.W., Hernández, L., Ripple, W.J., 2010. The landscape of fear: Ecological implications of being afraid. Open Ecol. J. 3 (1), 1–7.

Linden, D.W., Fuller, A.K., Royle, J.A., Hare, M.P., 2017. Examining the occupancy–density relationship for a low-density carnivore. J. Appl. Ecol. 54 (6), 2043–2052. https://doi.org/10.1111/1365-2664.12883.

Linnell, J., Salvatori, V., & Boitani, L. (2008). Guidelines for population level management plans for large carnivores in Europe. A Large Carnivore Initiative for Europe report prepared for the European Commission.

Linnell, J.D., Swenson, J.E., Anderson, R., 2001. Predators and people: Conservation of large carnivores is possible at high human densities if management policy is favorable. Anim. Conserv. 4 (4), 345–349.

Long, R.A., MacKay, P., Ray, J., & Zielinski, W. (Eds.). (2008). Noninvasive survey methods for carnivores. Island Press.

Macdonald, D.W., & Loveridge, A.J. (Eds.). (2010). The biology and conservation of wild felids. Oxford University Press.

MacKenzie, D.I., Bailey, L.L., 2004. Assessing the fit of site-occupancy models. J. Agric. Biol. Environ. Stat. 9 (3), 300–318.

MacKenzie, D.I., & Hines, J. (2023). RPresence: R interface for program PRESENCE (Version 2.13.48) [Computer software]. U.S. Geological Survey. ⟨https://www.usgs.gov/software/presence⟩.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83 (8), 2248–2255.

MacKenzie, D., Nichols, J., Royle, J., Pollock, K.H., Bailey, L., Hines, J., 2006. Occupancy Estimation and Modeling : Inferring Patterns and Dynamics of Species Occurrence xviii,, 324.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., & Hines, J.E. (2017). Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence (2nd ed.). Academic Press.

MACKENZIE, D.I., ROYLE, J.A., 2005. Designing occupancy studies: general advice and allocating survey effort. J. Appl. Ecol. 42 (6), 1105–1114. https://doi.org/10.1111/j.1365-2664.2005.01098.x.

Malpeli, K.C., Endyke, S.C., Weiskopf, S.R., Thompson, L.M., Johnson, C.G., Kurth, K.A., Carlin, M.A., 2024. Existing evidence on the effects of climate variability and climate change on ungulates in North America: A systematic map. Environ. Evid. 13 (1), 8.

McDougal, C., 1999. You can tell some tigers by their tracks with confidence. In: Seidensticker, In.J., Christie, S., Jackson, P. (Eds.), Riding the tiger: Tiger conservation in human-dominated landscapes. Cambridge University Press, p. 190.

McHenry, E., O'Reilly, C., Sheerin, E., Kortland, K., Lambin, X., 2016. Strong inference from transects sign surveys: Combining spatial autocorrelation and misclassification occupancy models to quantify the detectability of a recovering carnivore. Wildl. Biol. 22 (5), 209–216.

Mech, L.D., 1996. A new era for carnivore conservation. Wildl. Soc. Bull. 24 (3), 397–401.

Mekonen, S., 2020. Birds as a tool for ecosystem services and sustainable conservation. Cogent Food Agric. 6 (1), 1829374.

Ministry of Forests and Soil Conservation [MoFSC]. (2015). Strategy and action plan 2016–2025, Chitwan-Annapurna Landscape, Nepal. Ministry of Forests and Soil Conservation.

Morin, D.J., Yackulic, C.B., Diffendorfer, J.E., Lesmeister, D.B., Nielsen, C.K., Reid, J., Schauber, E.M., 2020. Is your ad hoc model selection strategy affecting your multimodel inference? Ecosphere 11 (1), e02997.

Odden, M., Athreya, V., Rattan, S., Linnell, J.D.C., 2014. Adaptable neighbours: Movement patterns of GPS-collared leopards in human dominated landscapes in India. PLOS ONE 9 (11), e112044. https://doi.org/10.1371/journal.pone.0112044.

Odden, M., Herfindal, I., Linnell, J.D.C., Andersen, R., 2010. Intraspecific variation in non-pedigree-based parentage assignment in a large carnivore. Behav. Ecol. Sociobiol. 64 (5), 757–767.

Odden, M., Wegge, P., 2005. Spacing and activity patterns of leopards Panthera pardus in the Royal Bardia National Park, Nepal. Wildl. Biol. 11 (2), 145–152.

Ordiz, A., Uzal, A., Milleret, C., Sanz-Perez, A., Zimmermann, B., Wikenros, C., et al., 2020. Wolf habitat selection when sympatric or allopatric with brown bears in Scandinavia. Sci. Rep. 10 (1), 9941.

ORNL DAAC, 2018. MODIS and VIIRS land products global subsetting and visualization tool. Oak Ridge Natl. Lab. DAAC. https://doi.org/10.3334/ORNLDAAC/1379.

Palomares, F., 2001. Vegetation structure and prey abundance requirements of the Iberian lynx: Implications for the design of reserves and corridors. J. Appl. Ecol. 38 (1), 9–18. https://doi.org/10.1046/j.1365-2664.2001.00565.x.

Paudel, R.P., Kadariya, R., Lamichhane, B.R., Subedi, N., Sashika, M., Shimozuru, M., Tsubota, T., 2022. Habitat occupancy of sloth bear Melursus ursinus in Chitwan National Park, Nepal. Ecol. Evol. 12, e8699. https://doi.org/10.1002/ece3.8699.

Pokheral, C.P., Wegge, P.J.E., 2019. Coexisting large carnivores: Spatial relationships of tigers and leopards and their prey in a prey-rich area in lowland Nepal. Écoscience 26 (1), 1–9. https://doi.org/10.1080/11956860.2018.1491512.

Poudel, S., Twining, J.P., Stedman, R.C., Ghimire, S.K., Fuller, A.K., 2023. Ecological and anthropogenic drivers of leopard (Panthera pardus fusca) attack occurrence on humans in Nepal. People and. Nature 5, 1977–1988. https://doi.org/10.1002/pan3.10536.

Prugh, L.R., Sivy, K.J., 2020. Enemies with benefits: Integrating positive and negative interactions among terrestrial carnivores. Ecol. Lett. 23 (6), 902–918. https://doi.org/10.1111/ele.13489.

Puri, M., Srivathsa, A., Karanth, K.K., Patel, I., Kumar, N.S., 2020. The balancing act: Maintaining leopard–wild prey equilibrium could offer economic benefits to people in a shared forest landscape of central India. Ecol. Indic. 110, 105931.

R Core Team. (2021). R: A language and environment for statistical computing (Version 4.2.1) [Computer software]. R Foundation for Statistical Computing. ⟨https://www.R-project.org/⟩.

Rabelo, R.M., Aragón, S., Bicca-Marques, J.C., 2019. Prey abundance drives habitat occupancy by jaguars in Amazonian floodplain river islands. Acta Oecologica 97, 28–33.

Riley, S.J., Degloria, S.D., 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermt. J. Sci. 5 (1–4), 23–27.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., et al., 2014. Status and ecological effects of the world's largest carnivores. Science 343 (6167), 1241484.

Ripple, W.J., Wolf, C., Newsome, T.M., Hoffmann, M., Wirsing, A.J., McCauley, D.J., 2016. Decline of the world's carnivores. Proc. Natl. Acad. Sci. 113 (5), 1081–1087.

Rostro-García, S., Kamler, J.F., Crouthers, R., Sopheak, K., Prum, S., In, V., et al., 2018. An adaptable but threatened big cat: Density, diet and prey selection of the Indochinese leopard (Panthera pardus delacouri) in eastern Cambodia. R. Soc. Open Sci. 5 (2), 171187.

Royle, J.A., Converse, S.J., 2014. Hierarchical spatial capture–recapture models: Modelling population density in stratified populations. Methods Ecol. Evol. 5 (1), 37–43.

Sari, A., Gündoğdu, E., Başkaya, Ş., Arpacık, A., 2020. Habitat preference by the Anatolian leopard (Panthera pardus tulliana Valenciennes, 1856) in north-eastern Anatolia, Turkey. Belg. J. Zool. 150. https://doi.org/10.26496/bjz.2020.78.

Seidlitz, A., Bryant, K.A., Armstrong, N.J., Calver, M.C., Wayne, A.F., 2021. Sign surveys can be more efficient and cost effective than driven transects and camera trapping: A comparison of detection methods for a small elusive mammal, the numbat (Myrmecobius fasciatus). Wildl. Res. 48 (6), 491–500.

Shehzad, W., Nawaz, M.A., Pompanon, F., Coissac, E., Riaz, T., Shah, S.A., Taberlet, P., 2015. Forest without prey: Livestock sustain a leopard Panthera pardus population in Pakistan. Oryx 49 (2), 248–253. https://doi.org/10.1017/S0030605313001026.

Sigdel, S., K.C, R.B., Karki, J.B., et al., 2025. Do habitat occupancy factors drive conflict with leopards (Panthera pardus) in the Mid–Hills region of Nepal? Eur. J. Wildl. Res. 71, 121. https://doi.org/10.1007/s10344-025-01999-0.

Singh, L.A.K. (2000). Tracking and monitoring of tigers and their prey: Practical manual for field biologists. Wildlife Institute of India.

Singh, R., Qureshi, Q., Sankar, K., Krausman, P.R., Joshi, B.D., Goyal, S.P., 2014. Distinguishing sex of free-ranging tigers using pugmark measurements. Ital. J. Zool. 81 (2), 304–309.

Smith, M.M., Erb, J.D., Pauli, J.N., 2023. Reciprocated competition between two forest carnivores drives dietary specialization. J. Anim. Ecol. 92 (9), 1695–1706. https://doi.org/10.1111/1365-2656.13962.

Spong, G., 2002. Space use in lions, Panthera leo, in the Selous Game Reserve: Social and ecological factors. Behav. Ecol. Sociobiol. 52 (4), 303–307.

Stein, A.B., 2020. Panthera pardus (amended version of 2019 assessment). IUCN Red. List Threat. Species. https://doi.org/10.2305/IUCN.UK.2020-1.RLTS.T15954A163991139.en.

Steinmetz, R., Seuaturien, N., Chutipong, W., 2013. Tigers, leopards, and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. Biol. Conserv. 163, 68–78.

Sutherland, C., Hare, D., Johnson, P.J., Linden, D.W., Montgomery, R.A., Droge, E., 2023. Practical advice on variable selection and reporting using Akaike information criterion. Proc. R. Soc. B 290 (2007), 20231261.

Takinami, H., Ishiyama, N., Takafumi, H., Kubo, T., Tomita, K., Tsujino, M., Nakamura, F., 2021. Young citizen sensors for managing large carnivores: Lessons from 40 years of monitoring a brown bear population. Conserv. Sci. Pract. 3 (9), e484. https://doi.org/10.1111/csp2.484.

Terraube, J., Van Doninck, J., Helle, P., et al., 2020. Assessing the effectiveness of a national protected area network for carnivore conservation. Nat. Commun. 11, 2957. https://doi.org/10.1038/s41467-020-16792-7.

Thapa, S., All, J., Yadav, R.K.P., 2016. Effects of livestock grazing in pastures in the Manaslu Conservation Area, Nepalese Himalaya. Mt. Res. Dev. 36 (3), 311–319.

Thapa, K., Malla, S., Subba, S.A., Thapa, G.J., Lamichhane, B.R., Subedi, N., Dhakal, M., Acharya, K.P., Karki Thapa, M., Neupane, P., Poudel, S., Bhatta, S., Jnawali, S. R., Kelly, M.J., 2021. On the tiger trails: Leopard occupancy decline and leopard interaction with tigers in the forested habitat across the Terai Arc Landscape of Nepal. Glob. Ecol. Conserv. 25, e01412. https://doi.org/10.1016/j.gecco.2020.e01412.

Thapa, K., Malla, S., Subba, S.A., Thapa, G.J., Lamichhane, B.R., Subedi, N., Dhakal, M., Acharya, K.P., Thapa, M.K., Neupane, P., Poudel, S., Bhatta, S.R., Jnawali, S. R., Kelly, M.J., 2021. On the tiger trails: Leopard occupancy decline and leopard interaction with tigers in the forested habitat across the Terai Arc Landscape of Nepal. Glob. Ecol. Conserv. 25, e01412. https://doi.org/10.1016/j.gecco.2020.e01412.

Thapa, K., Shrestha, R., Karki, J., Thapa, G.J., Subedi, N., Pradhan, N.M.B., Dhakal, M., Khanal, P., Kelly, M.J., 2014. Leopard Panthera pardus fusca density in the seasonally dry, subtropical forest in the Bhabhar of Terai Arc. Nepal, Adv. Ecol., 286949 https://doi.org/10.1155/2014/286949.

Theobald, D.M., Kennedy, C., Chen, B., Oakleaf, J., Baruch-Mordo, S., Kiesecker, J., 2020. Earth transformed: Detailed mapping of global human modification from 1990 to 2017. Earth Syst. Sci. Data 12 (3), 1953–1972. https://doi.org/10.5194/essd-12-1953-2020.

Tizzani, P., Bessone, M., Rossi, L., et al., 2022. Does predation risk affect spatial use in an introduced ungulate species? The case of a Mediterranean mouflon alpine colony. Eur. J. Wildl. Res. 68, 66. https://doi.org/10.1007/s10344-022-01611-9.

Twining, J.P., McFarlane, C., O′Meara, D., O'Reilly, C., Reyne, M., Montgomery, W.I., Helyar, S., Tosh, D.G., Augustine, B.C., 2022. A comparison of density estimation methods for monitoring marked and unmarked animal populations. Ecosphere 13 (10), e4165. https://doi.org/10.1002/ecs2.4165.

Wang, S.W., Macdonald, D.W., 2009. The use of camera traps for estimating tiger and leopard populations in the high-altitude mountains of Bhutan. Biol. Conserv. 142 (3), 606–613.

Watson, J.E.M., Shanahan, D.F., Di Marco, M., Allan, J., Venter, O., Jennings, W.D., Possingham, H.P., Atkinson, S., 2016. Catastrophic declines in wilderness areas undermine global environment targets. Curr. Biol. 26 (21), 2929–2934. https://doi.org/10.1016/j.cub.2016.08.049.

Widén, A., Cromsigt, J.P.G.M., Dressel, S., Felton, A.M., Singh, N.J., Widemo, F., 2023. Direct and indirect effects of food, fear and management on crop damage by ungulates. Ecol. Solut. Evid. 4, e12266. https://doi.org/10.1002/2688-8319.12266.

Wolf, C., Ripple, W.J., 2017. Range contractions of the world's large carnivores. R. Soc. Open Sci. 4 (7), 170052. https://doi.org/10.1098/rsos.170052.

Wolf, C., Ripple, W.J., 2018. Rewilding the world's large carnivores. R. Soc. Open Sci. 5 (3), 172235.

Yadav, S., Behera, S., Chatakonda, M.K., 2024. One size does not fit all: Differential predation on livestock species by leopards (Panthera pardus) in a multiuse landscape in the Gangetic plains, India. J. Nat. Conserv. 80, 126650. https://doi.org/10.1016/j.jnc.2024.126650.

Yoccoz, N.G., Nichols, J.D., Boulinier, T., 2001. Monitoring of biological diversity in space and time. Trends Ecol. Evol. 16 (8), 446–453. https://doi.org/10.1016/S0169-5347(01)02205-4.

Zhang, L., Li, Q., Kou, X., Ouyang, Z., 2022. Distributions of two native ungulates at the third pole are highly sensitive to global warming. Glob. Ecol. Conserv. 39, e02292.