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Habitat preference indicators for striped hyena (*Hyaena hyaena*) in Nepal

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ABSTRACT

The striped hyena (*Hyaena hyaena* Linnaeus, 1758) is one of the large carnivores of forest and grassland ecosystems across Africa and Asia and is currently threatened throughout its range. Hyena habitats are shrinking, due to the increase of human-dominated landscapes. The aim of this study was to identify hyena habitat use as indicated by visitation frequency in the human-dominated landscape of lowland Nepal. We followed a camera trap protocol for the estimation of hyena presence and visitation frequency. We used a generalized additive modelling approach with zero-inflated Poisson distribution to evaluate the effects of environmental variables on capture frequency. Our results showed that the two most important and significant predictors of hyena frequency data were canopy volume and maxD (the maximum among the shortest distances to water sources, agriculture land and villages). The highest hyena frequencies were in sites with low canopy volume, i.e. riverbeds and grasslands, whereas lower frequencies were observed in dense forests, i.e. acacia and riverine forests. Additionally, hyena frequency increased with increasing maxD up to 5–6 km and then dropped sharply at larger maxD values. Overall, our study suggests that hyenas prefer open landscapes along rivers and human settlements, where the following combination of conditions is met: adequate cover, access to food and water. The preservation of natural open landscapes close to human settlements and rugged hilly areas seems crucial for the long-term conservation of hyenas.

1. Introduction

Hyena species occupy a vast range of habitat types and fill a wide array of ecological niches, exhibiting remarkable ecological and social diversity (Hofer and Mills, 1998; Watts and Holekamp, 2007). The family Hyaenidae, one of the smallest among mammalian carnivores, now contains only four species: the striped hyena (*Hyaena hyaena*), the aardwolf (*Proteles cristata*), the brown hyena (*Hyaena brunnea*) and the spotted hyena (*Crocuta crocuta*) (East and Hofer, 1998; Hofer and Mills, 1998; Watts and Holekamp, 2007; Alam et al., 2015).

Among the four hyaenid species, only the striped hyena (hereafter hyena) is recorded in Asia (AbiSaid and Dloniak, 2015; Wolf and Ripple, 2017; Singh et al., 2014). It is one of the most important large scavengers with the ecosystem service role of

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removing carcasses and clearing off carrion in tropical ecosystems (Kruuk, 1976; Rieger, 1981; Hofer, 1998; Gupta et al., 2009; Bhandari et al., 2020,) that plays a major role in tropical forests and grassland ecosystems (Hofer and Mills, 1998; Kasparek et al., 2004; Wagner, 2006). This large carnivorous species distribution extends from the tropical and sub-tropical regions of East and Northeast Africa, through the Middle East and the Caucasus region, to Central Asia and into the Indian subcontinent (Kruuk, 1976; Hofer and Mills, 1998; Kasparek et al., 2004; Wagner, 2006). In this vast range, the hyena generally favors rocky and open landscapes within semiarid and arid ecosystems in the tropics, where water is available within 10 km and elevation is less than 3300 m above sea level (m.a.s.l.) (Prater, 1948; Kruuk, 1976; Roberts, 1977; Rieger, 1977, 1979; Heptner and Sludskii, 1980; Leakey et al., 1999; Wagner, 2006).

There is limited information on the species, and population abundance assessments are complicated; yet, it is clear that the species is already extinct in many localities (Kruuk, 1976; Hofer and Mills, 1998; Wagner, 2006; AbiSaid and Dloniak, 2015; Bhandari et al., 2020). There are historical references to the species since ancient times, and hyenas appear to feature prominently in Middle Eastern and Asian folklore (East and Hofer, 1998; Cogal et al., 2021). In 1998, total population size estimates ranged from ~4,000 to 13,000 individuals worldwide (Hofer and Mills, 1998; AbiSaid and Dloniak, 2015). Nowadays, however, the International Union for Conservation of Nature (IUCN) lists the hyena as near threatened (AbiSaid and Dloniak, 2015; Bhandari et al., 2015) as the species' global populations appear to follow an overall decreasing trend (Ripple et al., 2014; AbiSaid and Dloniak, 2015; Bhandari et al., 2020). Human activities are consistently indicated as the major source of mortality due to poisonings (Bhandari and Bhusal, 2017), wildlife-vehicle collisions (Adhikari et al., 2018) and direct persecution, which is seen as a means of retaliation for livestock depredation incidents, or associated with superstitious beliefs, folk magic and traditional medicine practices (East and Hofer, 1998; Hofer and Mills, 1998; AbiSaid, 2006; Tourani et al., 2012; AbiSaid and Dloniak, 2015). Across the hyena's wide global range, the current distribution is patchy and most populations are likely composed of small isolated groups that are vulnerable to local extinctions (Kasparek et al., 2004; Tourani et al., 2012; Wagner, 2006; Bhandari et al., 2020). Additionally, the species is considered as data deficient with limited ecological information and monitoring across its range (AbiSaid and Dloniak, 2015; Alam et al., 2015). Thus, there is a profound need for research to estimate population and habitat sizes as well as trends at multiple scales in order to develop and implement effective conservation plans.

In Nepal, hyenas are found in the lowlands of the southern part of the country and the estimated current population counts less than 100 individuals (Hofer and Mills, 1998; Bhandari and Chalise, 2016; Bhandari et al., 2020). The species is assessed as nationally endangered and consequently is protected by the Government of Nepal "National Park and Wildlife Conservation Act (NPWCA) 1973 (Bhandari et al., 2015). However, information on the species' past and present occurrence in the country as well as the factors affecting its populations are inadequate and hyenas still face numerous threats related to the human-hyena conflict and land use change (Bhandari and Chalise, 2016; Bhandari et al., 2020, 2021). In particular and regardless of the species' legal protection status, hyenas face high extinction risk in Nepal, due to rapid infrastructure development and human encroachment, which is also accompanied by increasing persecution of both hyenas and their prey (Hofer and Mills, 1998; Bhandari et al., 2021). In the present study, we explore the drivers of hyena habitat selection in the lowland geographical region of Nepal. Our aim was to determine the most significant factors underlying habitat use patterns in this human-dominated landscape in order to utilize this information in the development of effective conservation strategies in the future.

2. Materials and methods

2.1. Site description

Nepal is a country characterized by a diverse landscape with elevations of less than 100 m.a.s.l. in the south that reach up to 8848 m.a.s.l. in the Himalayas (Bricker et al., 2014). The study area is located at the South-Eastern lowlands of Nepal, (Fig. 1) about 200 km south of Kathmandu; an area that includes community managed government forests, corridor forests, rivers, agriculture lands and open hills and grasslands. Its elevation ranges between 80 and 800 m.a.s.l. The average temperature varies from 12°C in winter to 30°C in the summer (DFRS, 2014; Bhandari et al., 2020). Our study area is connected to the Parsa National Park to the West, serving as a major ecological forest corridor for large mammals such as the Asian elephant (*Elephas maximus*), the one-horned rhinoceros (*Rhinoceros unicornis*) and the Bengal tiger (*Panthera tigris*) (Smith and Mishra, 1992; Bhandari et al., 2015, 2020). The landscape is covered by mixed forests, riverine forests and tropical forests dominated by sal (*Shorea robusta*), acacia (*Acacia catechu*) and eucalyptus (*Eucalyptus* spp.) (Table 1). This area is home to more than 20 mammal species, 150 bird species, and 40 reptiles and amphibians (Chettri and Chhetry, 2013; Bhandari et al., 2015). Human inhabitants, which are ethnically diverse (*Tamang, Magar, Bhote, Tharu,* and *Maithali* ethnic groups), maintain relatively traditional lifestyles and depend mostly on forestry, agriculture and livestock. Lastly, the East-West highway (*Mahendra Highway*) crosses through the lowlands and divides the study area into plains (<300 m.a.s.l.) and hilly areas. The plains in the south are more densely populated in comparison to the hills in the north (CBS, 2012).

2.2. Hyena image frequency and environmental predictors

This study followed a systematic camera trap sampling. We superimposed a grid of 2 × 2 km and monitored all grid cells of four study regions [BA: arid environment, Sal forest dominant, connected to the Parsa national park; RA: mixed and acacia forest dominant; SA: Sal and eucalyptus forest dominant; MA: Sal and eucalyptus forest dominant]. At each sampling site, two camera traps were set to a tree or pole, one or two feet above the ground, and opposite to each other. Camera traps were set to

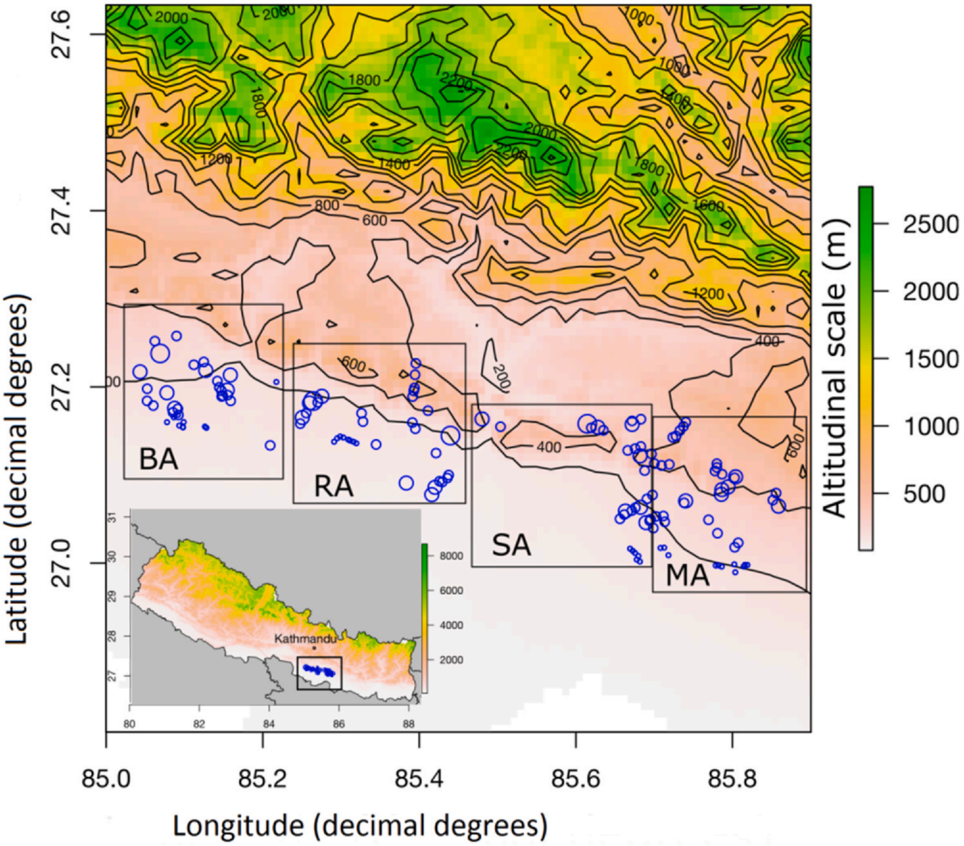

Fig. 1. Map of the study area in the lowlands of Nepal showing where the camera trap stations were installed. The locations where hyenas were camera trapped at least once are indicated by circles and the radii of the circles are proportional to hyena counts (visitation frequency) during the whole study period. The latitude and longitude are in decimal degrees and the altitudinal scale is in meters. The four sampling regions BA,RA,SA and MA are indicated by superimposed squares.

Table 1
Classification of the habitats of the study site in the lowland of Nepal.

Habitat type	Description	Percentage cover
Eucalyptus forest	This forest is dominated by *Eucalyptus* spp. including short grasses.	30%
Riverbed	It lies along the riverside and comprises small patches of sand, gravel or stone, grass and shrubs.	10%
Mixed forest	Temperate, deciduous and hardwood forests, such as Haldu (*Adina cordifolia*), Botdhainro (*Lagerstroemia parviflora*), Sisso (*Dalbergia sissoo*), Asna (*Terminalia alata*), Simal (*Bombax ceiba*), Siris (*Albizia* spp.), Kutmiro (*Litseamonopetala*), etc. This habitat also contains shrubs and tall grasses.	15%
Sal forest	Forest dominated by sal (*Shorea robusta*) with and mixture of Haldu and Asna trees.	25%
Acacia forest	Forest dominated by acacia species (*Acacia catechu*) and tall grasses.	5%
Riverine forest	It lies along the riverside along with acacia forests and comprises small patches of grass and shrubs.	10%
Grassland	Small patches of grassland, mostly Saccharum (*Saccharum* spp.) grasses with shrubs near to the edge of agricultural land, river or forests.	5%

operate with a trigger speed of 1 s in order to capture passing animals. After 14 trap nights, the camera traps were relocated, rotating systematically across the study area and the different habitat types in BA, RA, SA, and MA i.e. eucalyptus forest, riverbed, mixed forest, sal forest, acacia forest, riverine forest and grasslands (Table 1) with equal sampling effort. During this study, 28camera traps (model: The Stealth Cam 8 MP, G30 by ©Stealth Cam) were deployed in 144 sampling sites between December 2015 and November 2017.

Firstly, each hyena capture was listed as a single and independent sample, according to the relevant literature (Wagner, 2006; Gupta et al., 2009; Harihar et al., 2010; Singh et al., 2010). An individual may revisit a location within its territory or home range once every one to two weeks (Kruuk, 1976; Hofer and Mills, 1998; Wagner, 2006). We followed the published guidelines to distinguish individual hyenas based on stripe pattern (Wagner, 2006; Gupta et al., 2009; Harihar et al., 2010; Singh et al., 2010; Tichon et al., 2017) and if the same individual was captured more than once within 24 h, we considered only one of the images as a sample for the analysis. Capture date, time and location were embedded in each photo, thus enabling cross-referencing. Hyena visitation frequency per site is expressed as counts per trapping period (14 trap nights).

Environmental variables such as habitat type, canopy coverage, coordinates of trapping site, were recorded within the 2 × 2 km grid cells. We calculated distance attributes like distance to the closest roads, water sources, agriculture land and villages/city, using GPS coordinates of each camera trap station in QGIS (version 3.2). We used a crown densitometer to estimate the percentage of canopy cover (Lemmon, 1956; Cook et al., 1995; Korhonen et al., 2006) and then, we defined four canopy volume classes: No Coverage (NC, canopy cover = 0), Low Coverage (LC, canopy cover between 10% and 49%), Moderate Coverage (MC, canopy cover between 50% and 69%) and High Coverage (HC, canopy cover over 70%). Following a data driven approach, we also set a new composite variable that provided good model fits: maxD [the maximum value among the following: Distance to the closest water source (DW), Distance to the closest agriculture land (DA) and Distance to the closest village/city (DV)]. The values of maxD indicate that a water source, an agricultural land unit, and a village unit are all included within a radius of maxD around the sampling site. Thus, the interpretation of maxD is that it defines the minimum distance within which all possible requirements for hyena's activity, namely the existence of agricultural land, villages and water, are fulfilled.

2.3. Statistical analysis

Our data refer to the number of hyena images taken at each camera trap station at a specific time period of camera operation. Hereon, we refer to this number as hyena counts. For evaluating the influence of possible predictors on hyena counts, we used generalized additive models (gams) with the negative binomial distribution family to account for possible over dispersion. We used gams for their flexibility to fit nonlinear responses by smoothing. The mgcv package was used (Wood et al., 2016) in R (R Core Team, 2020) for fitting gams. We followed a sequential modelling approach conceptually similar to the hierarchical modelling described by Diaz et al. (2007), de Vries et al. (2012), de Vries et al. (2013) and Mpokos et al. (2014). Groups of possible predictors were used sequentially. The first group includes large-scale descriptors of the spatial arrangement of camera trap stations, such as sampling region, altitude and a set of spatial filters. Sampling region was included as a random factor to account for the repetition of sampling in each region, as well as for summarizing possible long-term effects of factors like local climate, geology, hydrology and management that might have affected hyena population distribution historically in ways that are difficult to evaluate otherwise. Spatial filters that describe the spatial configuration of trap stations were used to account for possible spatial autocorrelation of hyena counts.

We produced spatial filters using the function *meigen* of the *spmoran* package in R (R Core Team, 2020). The function implements the Moran's autocorrelation index maximization method of Dray et al. (2006). We set spatial filters and altitude as smooth terms to build gams of increased complexities. We then selected the most parsimonious model for the first group of predictors using the AIC estimated by the mgcv package (see Wood et al., 2016) as the selection criterion. The second group of predictors were quantitative and qualitative descriptors of vegetation around camera trap stations. Quantitative descriptors were the canopy cover (as a continue value) and the canopy volume (a factor with four levels). Habitat type, a qualitative vegetation descriptor, was included as a random factor.

We preferred to include the quantitative (or discretised quantitative) descriptors of the vegetation as fixed factors and habitat identity as a random factor, since the former can provide (if significant) a more general model that can possibly predict the response outside the specific study region. The inclusion of habitat type as a random factor is also a choice that keeps the model general enough, although habitat types were selected according to their frequency and not randomly.

The interaction of vegetation descriptors with sampling season was also included in this group. The selected terms from the first step were retained in the model when terms from the second group were added. The last set of predictors were the shortest distances to landscape elements like roads, agricultural land, villages, water sources as well as maxD. Interactions between terms of this third group with sampling season and with the vegetation descriptors were checked at this step. The rationale behind fitting groups of terms sequentially keeping the hierarchy (the spatial scale in our case) is that the variables that were added later in the modelling process were unlikely to influence those that had been previously added (de Vries et al., 2013). The sequential fitting ensures that ultimate causes were added before other possible predictors that might be affected by the former. If the ultimate factors account for most of the variation of the response, then more proximate factors would not improve model likelihood when added (de Vries et al., 2013). As a final step to build a parsimonious model, we checked if all the terms included provided a significant fit. We removed the not significant terms one by one based on the effect the removal had on the AIC of the resulted model. The final model was checked for pairwise concurvity among the smooth terms. Concurvity is a generalization of collinearity to describe nonlinear dependencies among the smooth terms of a gam model. Concurvity can introduce bias in the estimation of model parameters and underestimation of their variance, producing an inflated type 1 error. Furthermore, in gams there are severe computational problems in the presence of concurvity (Wood, 2008). However, the concurvity driven variance bias is avoided if the computational difficulties are solved (Wood, 2008). Thus, the computational methods proposed by Wood (2008), as implemented in mgcv, minimize the variance bias due to concurvity, given that the model fit solution converges. For visualizing significant interactions involving smooth terms of the model we used *itsadug* package (van Rij et al., 2020).

3. Results

The highest value of hyena counts was recorded in the No Cover class of canopy volume that includes grasslands and riverbeds (Fig. 2). The number of hyena captures over the study period varied between 1 and 8 (average 4.8) in grasslands and between 3 and 8 (average 5.5) in riverbeds. The three other cover classes contain mainly sal and mixed forests. The High Cover class includes riverine and acacia forests while in the Low and Medium Cover classes there were eucalyptus but not riverine

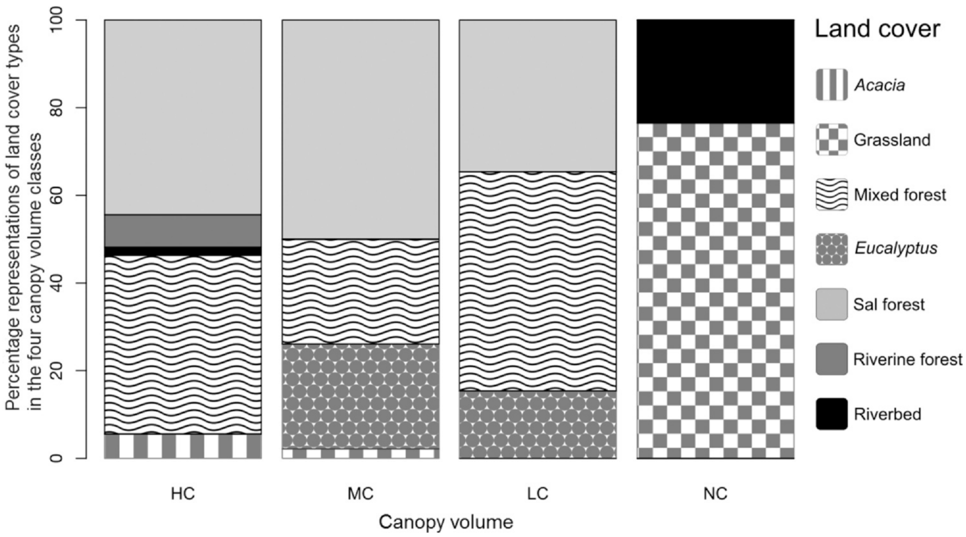

Fig. 2. Proportional representation of forest types in the four Canopy Volume classes. HC = High coverage, MC = Moderate coverage, LC = Low coverage, NC = No coverage.

forests. There are considerable variations in hyena frequency by habitat type (Fig. 3) which partially explain the variation by canopy volume. High observation frequencies were at riverbeds and grasslands that belong to the No Cover class. Observation frequencies of hyenas in acacia and riverine forests, that are included in the High Canopy Volume class, are rather high. Notably, hyenas are apparently missing from eucalyptus forests, which were included in the low and Moderate Canopy Volume classes.

The data provided in Table 2 summarize the major steps towards the construction of a gam model for hyena counts data. We started with a null model with only the region as a random factor. The best model, after introducing the spatial filters and altitude, was one that included three spatial filters. Adding vegetation properties, the model improved when habitat type was included as a random factor and canopy volume as a fixed factor (parametric). The interactions of the habitat type and/or the canopy volume with season were not significant and increased the AIC of the produced models. Interaction terms were dropped. In the final step, the most parsimonious model included maxD and the interaction of maxD with season and canopy cover. Alternative models including distance to roads or models produced by substituting maxD by any of its constituent distances had higher AIC values. The best of the alternative models (with only 8.6 AIC units increase) was obtained when maxD was substituted by distance to agricultural land. Note that maxD values are mostly determined by distance to agricultural land. In 59.2%

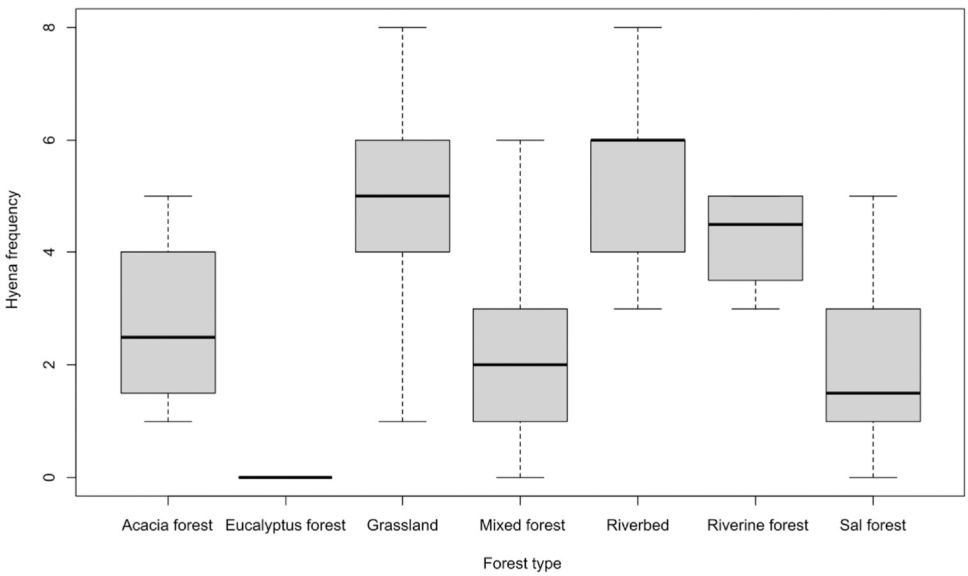

Fig. 3. Hyena observation frequencies (percentage of total hyena image in the different habitats over the study period) by forest type. Box: Q2 = median, Q1 = 25% and Q3 = 75% percentiles. Whiskers: Lower = Q1−1.5IQR and Upper = Q2 + 1.5IQR, IQR = Q2-Q1.

Table 2
Akaike's information criterion (AIC), log likelihood values (logLik), estimated degrees of freedom (df), estimated dispersion and % deviance explained by the gam models fitted to hyena count data.

GPPs	Term included in the model	AIC	Aicdif	LogLikehood	df	dispersion	% deviance explained	R^2 (adj)
I	Region	550.9	154.4	−274.3	2.00	0.92	0.00	0.00
I	+Spatial filters SF2,SF3,SF4	515.4	114.1	−250.5	8.80	1.10	28.4	0.18
II	+Habitat Type	453.5		−218.6	9.76	0.83	49.9	0.47
II	+CV	446.6		−212.3	13.2	0.76	54.6	0.53
III	+maxD	407.0		−192.9	12.9	0.61	68.9	0.61
III	+maxD:CV +maxD:season	393.9		−182.6	17.5	0.51	76.7	0.70

The models were produced sequentially by fitting three groups of possible predictors (GPPs) (I. large scale spatial descriptors, II. vegetation properties and III. distances to landscape units), using AIC to select the most parsimonious model at each step. Only models that minimized AIC for each group of predictors are presented.

of the camera trap stations the distance to agricultural land was bigger than that to water sources and villages. Distance to villages was bigger than the other two in 37.6% of cases and distance to water was bigger in the remaining 3% of the cases. At the final step of the model building approach, the spatial filters were removed since their effect was not significant and the AIC of the model was decreased after their removal. Pairwise concurvity tests of the selected model indicated some cases of nonlinear dependencies between smooth terms, specifically between Habitat type and the maxD by NC canopy volume interaction term (concurvity estimated maximum= 0.46) and between maxD and the maxD by MC canopy volume class (concurvity estimated maximum = 0.50). This, rather moderate concurvity is considered having a minor effect on model parameter estimation since the model converged (see Wood, 2008).

Table 3
Summary statistics of the gam model predicting hyena frequency.

Parametric coefficients					
	Estimate	Std Error	Z value	P value	Sig. Level
Intercept	0.163	0.289	0.563	0.573	
Canopy volume = Low	−0.321	0.201	−1.600	0.110	
Canopy volume = Moderate	−0.493	0.218	−2.267	0.023	*
Canopy volume = No Cover	1.414	0.448	3.160	0.002	**
Reference category = High					
Approximate significance of smooth terms					
	edf	Ref.df	X^2	P value	Sig. Level
maxD	1.846	2	18.666	0.001	**
maxD by season					
season = Autumn	0.526	3	1.168	0.146	
season = Spring	0.000	3	0.000	0.483	
season = Summer	1.582	3	11.795	0.001	**
season =Winter	0.000	3	0.000	0.253	
maxD by canopy volume					
Canopy volume = High	0.000	3	0.000	0.369	
Canopy volume = Low	0.000	3	0.000	0.618	
Canopy volume = Moderate	0.580	3	1.458	0.126	
Canopy volume = No Cover	1.587	3	14.871	0.003	**
Random factors					
region	0.000	3	0.000	1.000	
Habitat type	4.148	6	10.906	0.018	*
Intercepts, standard errors and 95% confidence interval limits for Habitat type					
Habitat type	Estimate	SE	Lower 25%	Upper 97.5%	
Acacia forest	0.121	0.313	−0.493	0.734	
Eucalyptus Forest	−0.782	0.386	**−1.54**	**−0.026**	
Grassland	−0.105	0.335	−0.762	0.552	
Mixed forest	0.186	0.246	−0.295	0.668	
Riverbed	0.125	0.316	−0.494	0.745	
Riverine forest	0.5	0.298	−0.085	1.08	
Sal Forest	−0.045	0.25	−0.535	0.446	
R^2 (adj) = 0.695, Deviance explained = 76.30%.					

Coefficients, standard errors, z values, and significance of parametric effects, effective degrees of freedom (edf), reference degrees of freedom (Ref. df), chi squared values (X^2) and significance of smooth terms.

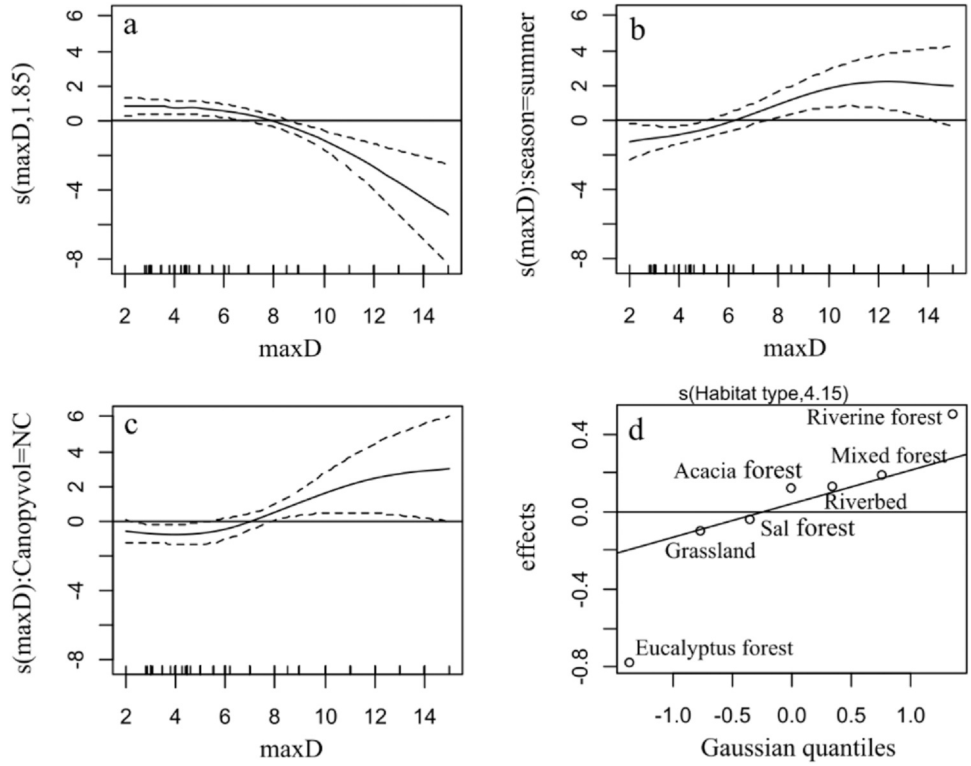

Fig. 4. Partial effects plot of the significant smooth terms and random effects of the model fit to hyena count (image frequency) data. a) maxD, b) interaction of maxD with season = Summer, c) interaction of maxD with canopy volume = No cover and d) intercepts of the random factor Habitat type. maxD is the maximum among the shortest distances to villages, agricultural land and water sources. Tick marks on the horizontal axis indicate observed data points. The vertical axis represents the partial effect of each smooth term indicating the contribution of each model term on the estimation of Hyena counts, fixing all other terms involved at their mean value.

The summary statistics of the selected generalized additive model are given in Table 3. The model explains 76.3% of the deviance of hyena count data. There is a significant variation of hyena counts by canopy volume (parametric term). The model predicts intermediate values for the low and high canopy volume levels, significantly higher values for the no cover level and significantly lower values for the moderate canopy volume level. Among the smooth terms maxD and the interactions of maxD with canopy volume and season were the most important and significant predictors of hyena count data. Habitat type (random effect) was also significant; an effect that is due to the low average predicted for eucalyptus forests (intercept = −0.782, SE = 0.386, 95% CI = −1.54 to −0.026).

Partial effect plots of the significant model terms are provided in Fig. 4. Hyena counts decrease nonlinearly with maxD. They are predicted to be higher than the overall average at places where the shortest distance to water, agricultural land and villages was less than 8 km (maxD <8, Fig. 4a). At greater distances, hyena counts are predicted to be lower than average and decrease sharply with increasing maxD. This general pattern holds for all seasons but summer (Fig. 4b) and for all canopy volume classes but in the no cover class (Fig. 4c). In both cases the animals seem to spread over higher distances as positive (above average) effects were obtained when maxD was greater than 6 and 7 km respectively. The effect of habitat type (Fig. 4d) is significant because the predicted intercept for the eucalyptus forests was significantly lower than zero. It is to be noted however, that sampling sites in eucalyptus forests were far from either villages or agricultural land or water sources (average maxD = 10 km, when for the other land use types it was less than 6 km with a minimum of 4.5 km for riverbeds) and very close to roads (average = 1.05 km, compared to 1.54 km for riverbeds, the second closest to roads land use type and to the maximum of 4.25 km for acacia forests).

To visualize model predictions, we provide in Fig. 5 how hyena counts are predicted to vary with maxD by canopy volume during winter (Fig. 5a) and by season (Fig. 5b) for the high canopy volume class. There is a major difference between the no canopy and the other classes of canopy volume both regarding the number of counts (higher in the no cover class) and the pattern of response against maxD. In the no canopy class hyena counts are predicted positive for a wide range of maxD values (up to 14 km) with a maximum value at about 9.5 km. In all other cases hyena counts were predicted positive for a narrow maxD range (0–8 km). A similar difference is observed between summer and all other seasons (Fig. 5b). It is predicted that during

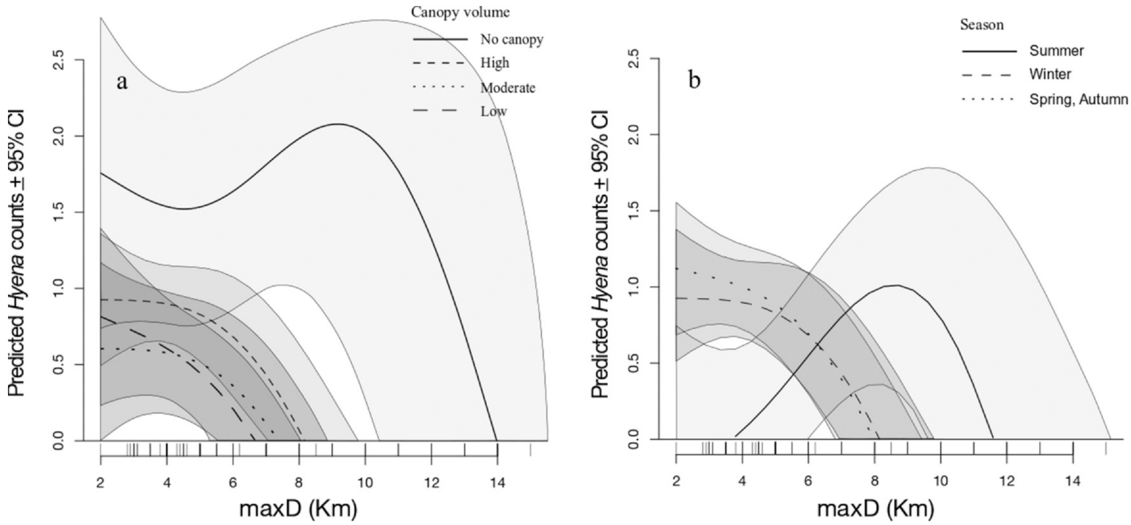

Fig. 5. Predicted counts (average and confidence intervals) of hyena in response to maxD by a) canopy volume, setting season to winter, and b) season, setting canopy volume to High. For both predictions region was set to BA and Habitat type to sal forest. maxD is the maximum among the shortest distances to villages, agricultural land and water sources.

summer hyenas were active at a range of maxD values between 4 and 12 with a maximum at about 8.5 km, while in other seasons hyena counts were predicted positive for a maxD range between 0 and 8 km.

4. Discussion

This study reported considerable variations in hyena frequency by habitat type. These findings corroborate previous reports, where hyenas prefer open semi-arid, arid habitats and dry forests (Rieger, 1979, 1981; Wagner, 2006; AbiSaid and AbiSaid, 2007; Gajera et al., 2009; Alam et al., 2015). We found that hyenas tend to use less forested habitats located rather close to human modified environments. Kuhn (2005), Alam et al. (2015) and Bhandari et al. (2020) reported that hyenas seemed to roam significantly more frequently in the hilly areas (around 200–400 m.a.s.l.), composed of low forest cover and more open, semi-arid and rocky habitats with available water sources (Hofer and Mills, 1998). This type of habitat has also been considered as favorable for many ungulates and small mammals, which compose the main prey species for hyena (Kerbis-Peterhans and Horwitz, 1992; Qarqaz et al., 2004; Kuhn, 2005; Gajera et al., 2009; Alam and Khan, 2015). Bhandari et al. (2020) reported that in semi-arid environments, mixed forests and hilly areas are also a refuge for many medium sized prey species.

The landscape surrounding our sampling sites includes several open space areas near hills, rivers and forest patches (Bhandari and Chalise, 2016; Bhandari et al., 2020). The grasslands include wide open habitat that is characterized by small shrubs, bushy areas and grass type ecosystems dominated by Kans grass (*Saccharum spontaneum*) and Sabai grass (*Eulaliopsis* spp.). Our results showed that hyenas are more commonly encountered in such habitats than dense forests. They also align with Rieger's records which list the following habitats as important for the species: savannas, semi-arid areas, mountainous areas with rough topography, deep valleys with shelters, caves, hillsides with little or no vegetation and riversides (Rieger, 1979). Other studies also support that hyena presence is positively correlated with grass availability and negatively correlated with tree density (Alam et al., 2014), while the species seems to select small hills, narrow valleys and open terrains (Akay et al., 2011).

Hyenas may settle in areas where three basic needs are met; i.e. sufficient food supply, adequate cover and access to water (Kruuk, 1976; Qarqaz et al., 2004; Hofer and Mills, 1998; Singh et al., 2010). Accordingly, our results show that hyenas select habitat that is at most within 8 km from human settlements, agricultural land and any source of water. Previous studies confirm that water accessibility plays a major role in habitat selection (Alam et al., 2014) and find that the species needs a water source within 10 km (Rieger, 1979; Wagner, 2006). However, in open habitats, like grasslands and riverbeds and during the summer, hyena activity appears to spread at considerably larger distances from human settlements and water sources than in other habitat types and seasons. This may be attributed to human disturbance (i.e. livestock grazing/forest fires/logging, etc.) which more or less increases in summer and could possibly affect both hyenas and their prey species near human settlements. Illegal hunting is also more frequent during the summer and hunters are mostly active around human settlements where visibility is higher.

Still, a number of studies indicate that hyenas are observed near human settlements (Prater, 1948; Kruuk, 1976; Hofer and Mills, 1998; Singh et al., 2010; Akay et al., 2011; Alam et al., 2014), as well as around urban areas (AbiSaid and AbiSaid, 2007; Akay et al., 2011), due to foraging opportunities (Alam et al., 2014; Akay et al., 2011; Singh et al., 2010). The species can easily feed on domestic waste in refuse and garbage dumps (AbiSaid and AbiSaid, 2007; Alam et al., 2014), livestock farms (e.g. poultry farms), slaughter houses (AbiSaid and AbiSaid, 2007), and lastly, livestock carcasses (AbiSaid, 2006; AbiSaid and AbiSaid, 2007;

Singh et al., 2010; Akay et al., 2011; Alam et al., 2014). Free-grazing livestock, e.g. cattle, goats and sheep, frequently displays high mortality rates (Singh et al., 2010; Bhandari et al., 2020). Inadequate veterinary care and semi starvation conditions, in combination with avoidance of meat consumption by humans for religious reasons, result in abundancy of available and unexploited carcasses in the proximity of humans (AbiSaid, 2006; Singh et al., 2010; Bhandari et al., 2020). Nevertheless, hyenas avoid interaction with humans (Wagner, 2006; Alam et al., 2015), as they are vulnerable to persecution by humans and predation by feral dogs, especially during daylight hours (Hofer and Mills, 1998; Singh et al., 2010).

Furthermore, rugged habitats are suitable for shelter, enabling hyenas to select for large caves and dens (Rieger, 1979; Leakey et al., 1999; Wagner, 2006; Singh et al., 2014). They can sustain higher hyena densities (Wagner, 2006; Singh et al., 2010), which may also explain the use of mixed forests and other habitats in the more mountainous parts of the study area in the present survey. Such refugia for safe den and resting sites, may be caves and rocky ridges, because steep terrain is unsuitable for agriculture or other human activities, as well as, not easily accessible for humans and dogs and hence, "unattractive" (Singh et al., 2010; Alam et al., 2014). Such natural habitats free of anthropogenic disturbances that can act as refuge for the hyenas are crucial for source populations (East and Hofer, 1998; Kolowski and Holekamp, 2006; Singh et al., 2010; Bhandari and Bhusal, 2017; Bhandari et al., 2020).

The results of this study also suggest that the hyenas select riverine and acacia forests over eucalyptus forests. A positive correlation of the species' presence with acacia forests has been recorded before by Alam et al. (2014) who find *Acacia-Tectona/Anogeissus* forests to be an important factor in terms of habitat suitability in western India (Alam et al., 2014). On the other hand, the negative correlation with eucalyptus forests could be not an avoidance of the forest type, but avoidance of roads or other points of threat/pressure. This result could also be attributed to the fact that eucalyptus forests are just too far away from the other two prerequisites that are food and water sources.An alternative hypothesis for the absence of hyena from eucalyptus forests is that those forests are like monocultures forming a uniform landscape with low species diversity, and probably low prey species abundance. If the latter is correct, such monoculture forests maybe a major threat for hyenas in the future; nevertheless, the present study is unfit to verify this hypothesis and a specifically designed studies are needed.

5. Conclusions

In this study, we concluded that environment and human presence and activities shape hyena distribution in the south-eastern lowlands of Nepal. High hyena frequencies in grasslands and riverbeds in proximity to human settlements and water sources are mostly attributed to food and water availability, while the preference for the more rugged landscape (200–400 m.a.s.l.) is attributed to safe refuge availability. The reasons for the absence of hyenas from eucalyptus forests are not clear but may be linked to the monoculture character of the forest and the consequent low prey abundance. If so, low plant diversity may be a major threat for hyenas and land use change towards monoculture exploitations a driver of local extinctions. Overall, populations of this large scavenger appear to be declining worldwide and the lack of adequate information makes it extremely difficult to design and implement appropriate conservation strategies. It is crucial to conduct further research to better understand habitat selection patterns, identify threats and pressures and ultimately, design and adopt an effective conservation strategy to ensure the species' survival.

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.

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