Spatial segregation between wild ungulates and livestock outside protected areas in the lowlands of Nepal

Shivish Bhandari¹, Ramiro Crego², and Jared Stabach³

¹Himalayan Biodiversity Network Nepal ²University of North Texas ³Smithsonian Conservation Biology Institute

September 11, 2020

Abstract

Understanding how wildlife interacts with human activities across non-protected areas are critical for conservation. This is especially true for ungulates that inhabit human-dominated landscapes outside the protected area system in Nepal, where wildlife often coexist with livestock. Here we investigated how elevation, agricultural land, distance from roads, and the relative abundance of livestock influenced wild ungulate (chital (Axis axis), nilgai, barking deer (Muntiacus muntjak), wild boar (Sus scrofa) and sambar (Rusa unicolor)) abundance and occurrence. We counted all individuals of wild ungulates and livestock along 35 transects conducted between November 2017 and March 2018 in Bara and Rautahat forests in the lowlands of Nepal. We assessed abundance and occurrence relation to covariates using Generalized Linear Models. We found that livestock outnumbered wild ungulates 6 to 1. Wild boar was the most abundant wild ungulate, followed by nilgai, chital, barking deer and sambar. We found that elevation and livestock abundance were the most important covariates affecting the overall abundance of wild ungulates and the distribution of each individual ungulate species. Our results suggest spatial segregation between wild ungulates, which occur mainly on highlands, and livestock that concentrate across lowland habitats. Our results provide critical information to improve conservation in community forest areas of Nepal, where wildlife interacts with people and their livestock. Finding better strategies to allow the coexistence of ungulates with people and their livestock is imperative if they are to persist into the future.

Introduction

The global environmental crisis is pushing a myriad of species to the brink of extinction (Cardillo et al., 2004; Ceballos et al., 2020; Román-Palacios & Wiens, 2020). Among the most vulnerable species are large terrestrial mammals (Craigie et al., 2010; Ceballos et al., 2017; Ceballos & Ehrlich, 2002), particularly herbivores (Atwood et al., 2020), which have experienced sharp population declines due to the ongoing and massive anthropogenic pressure on terrestrial ecosystems. Over the next 50 years, the global human population is expected to exceed 10 billion (Lutz et al., 1997; Lutz et al., 2001), putting increasing pressure on ecosystems. Whereas, formal protected areas play a vital role in conserving biodiversity (Wittemyer et al., 2008; Aziz et al., 2017), only a few are large enough to encompass the ecological and territorial needs to sustain large mammal populations (Ceballos et al., 2017; Newmark, 2008). As a result, most terrestrial large mammal migrations are in sharp decline or already extinct (Berger et al. 2004; Harris et al., 2009). Moreover, protected areas tend to concentrate human population density at their edges (Wittemeyer et al., 2008; Veldhuis et al., 2019), restricting animal mobility and leading to increased human-wildlife conflict, including increased incidences of poaching, and competition and/or predation of livestock (Woodroffe & Ginsberg, 1998; Wittemyer et al., 2008; Western et al., 2009; Craigie et al. 2010; Ripple et al. 2016). Finding solutions that ensure the coexistence of wildlife with humans, especially across areas with no form of environmental

protection, is crucial for the future of conservation of these species (Western et al., 2009; Ceballos et al., 2017).

In developing countries, rural poverty tends to increase the demand for access to natural resources (Sodhi et al., 2010; Shrestha & Bhawa, 2013; Shrestha et al., 2018). Forests are among the most impacted of all ecosystems. Forest loss has been particularly pervasive in Asia. Supporting ~9% (about 700 million) of the global human population (Poffenberger, 2006; Chao, 2012), Asia has experienced high deforestation rates (> 300 km^2 /year; Hansen et al., 2013). Most forests are cleared to increase the size of pastures for increasing densities of livestock (Sodhi et al., 2010; Squires, 2014), resulting in consequential large-scale declines in local biodiversity (Ceballos & Ehrlich, 2002; Brook et al., 2003; Sodhi et al., 2004; Xu et al., 2009; DiMarco et al., 2014). Currently, one-quarter of all Asian mammal species are now threatened with extinction and in urgent need of improved conservation strategies (Schipper et al., 2008), including ungulate species such as pygmy hog (*Porcula salvania*), Indian mouse deer (*Moschiolaindica*), swamp deer (*Cervus duvaucelii*), gaur (*Bos gaurus*), and four-horned antelope (*Tetracerus quadricornis*) (IUCN, 2020). To protect large mammals, conserving large tracts of mature forests across human-dominated landscapes is crucial (Halladay & Gilmour, 1995; Sodhi et al., 2010).

Nepal is home to a wide diversity of habitats, from tropical ($^{2}200 \text{ m}$) to alpine (> 4000 m) systems, supporting an incredible array of species. Formal protection for these habitats, however, is severely limited, with only 14% of the land surface currently under any form of protection. Over half of all ungulate species are threatened with extinction (Karki, 2011; Allendorf et al., 2020). Approximately 29% of the forested land in Nepal (areal estimate >16,000 km²) is managed under community forestry practices by local and state entities (DFRS, 2015; Acharya et al., 2016; Shrestha et al., 2018). The annual rate of forest loss across these areas was 0.9%, or approximately 28 km² per year for the period between 2001 and 2016 (Shrestha et al., 2018). Human population is also on the rise, leading to concomitant increases in livestock (Poudel & Kindlmann, 2012; Khadka, 2017). This has raised conservation concerns as livestock spatially displace wild ungulates, forcing wildlife to forage in low-quality food areas via exploitative and interference competition, and leading to reduced fitness (Mishra et al., 2004; Khadka, 2017). Once ungulates are displaced from natural forests, they increasingly occur in agricultural areas, increasing crop damage and leading to conflict with farmers (Ballari & Barrios-Garcia, 2014; Khanal et al., 2018). This conflict has, for instance, decreased population abundance of the nilgai (*Boselaphus tragocamelus*) across Nepal (Khanal et al., 2018).

Understanding the relationship between ungulates and the environment can contribute to the sustainable management of these species, items that are critical for the conservation of Nepal's megafauna (Smith et al., 1998; Weggee et al., 2009; Paudel & Kindlmann, 2012). To date, comparatively little attention has been paid to how anthropogenic pressure, including farmers and their livestock, drive the distribution and habitat selection of ungulates outside Nepalese protected areas. In this study, we investigated how elevation, agricultural land, distance from roads, and the relative abundance of livestock influenced the abundance and occurrence of wild ungulates (chital (Axis axis), nilgai, barking deer (Muntiacus muntjak), wild boar (Sus scrofa) and sambar (Rusa unicolor)), with the goal of providing information to help design more sustainable practices to ensure the sustainable coexistence of wild species and people that are dependent on these ecosystems for survival.

Materials and methods

Study area

This study was conducted across an approximate 300 km²region in the lowlands of central-eastern Nepal (26.9-27.4° N; 84.9-85.2° E) (Fig. 1). The terrain is hilly, with an elevation range of 80 to 800 m.a.s.l. The landscape is covered by tropical forest, dominated by Sal (*Shorea robusta*) and acacia (*Acacia catechu*) species. The area borders Parsa National Park to the west, the Mahabharat mountains to the North, agricultural lands and human settlements to the south, and other community forest and scattered human settlement to the east (Fig. 1). Most of the local people in this area rely on agriculture and livestock farming for subsistence. The main crops are corn (*Zea mays*), wheat (*Triticum aestivum*), potato (*Solanum*)

tuberosum), and rice (Oryza sativa). Main livestock species include cattle (Bos taurus indicus), buffalo (Bubalus arnee), goats (Capra hircus), and sheep (Ovis aries). Forest products, harvested for subsistence, include firewood, leaves, and wood.

These community forests are home to more than fifty mammalian species including large predators (e.g., tiger (*Panthera tigris*), common leopard (*Panthera pardus*), and striped hyenas (*Hyaena hyaena*)), mega herbivores (e.g., Elephants (*Elephas maximus*), one-horned rhinoceros (*Rhinoceros unicornis*)), and large herbivores (e.g., chital, nilgai, barking deer, wild boar and sambar) (Karki, 2011; Allendorf et al., 2020; Bhandari et al., 2020). In this study, we focused specifically on the effects on chital, nilgai, barking deer, wild boar, and sambar. Importantly, our study site is one of the major corridors for elephants and a core habitat range in Nepal for tiger (Smith and Mishra, 1992; Smith et al., 1998; Bhandari & Chalise, 2016).

Data collection

Between November 2017 and March 2018, we conducted 35 line transects to count the number of four species of livestock (goats, sheep, cows and buffalo) and five wild ungulate species (chital, wild boar, sambar, nilgai and barking deer). Transect starting locations were selected randomly across the study area. Because of terrain difficulties, transects length varied (mean transect length = 1648 m \pm 496 SD; range = 573 to 2799 m). Transects were spaced > 2 km apart to maintain independence (Fig. 1). All aforementioned wild and domestic animals present within 100 m from the center of the transect were counted.

We incorporated a set of covariates that we thought *a priori* could affect the abundance and occurrence of these ungulate species. The study area presents a marked north-south elevation change. Thus, we included mean elevation for each transect, derived from a 90-m digital elevation model (Farr et al., 2007). To account for the effect of roads on species occurrence, we obtained road information from the Nepalese Department of Survey (Kathmandu, Nepal), given the recognized importance of roads in adversely affecting ungulate occurrence across the region (Benítez-López et al., 2010). To account for the potential effect of agricultural areas, we manually digitized all agricultural patches identified using high resolution Google Earth imagery (Google Inc., Mountain View, CA, USA) using QGIS 3.12.1 (QGIS Development Team, 2009). We estimated the mean Euclidean distance of each transect to the nearest river, road or agricultural area (Fig A1). We used the raster package in R for all geospatial analyses (R Development Core Team, 2016).

To account for the potential effect of livestock on large herbivores (Hempson et al., 2017), we calculated the total number of individuals of all four species of livestock counted along the transect and divided this value by the length of the transect (ind/km), providing a transect-level measure of relative abundance.

Statistical analysis

We used generalized linear models (GLMs) with a Poisson distribution to investigate the factors explaining ungulate abundance across the landscape. We used an offset (log of transect length) to account for different sampling efforts due to different transect lengths (Kery, 2010). We modeled ungulate abundance in relation to distance to roads, distance to agricultural fields, elevation, and livestock relative abundance. For this analysis, we added the counts of all ungulates to evaluate how the community responds to each of the different covariates.

Additionally, we investigated single species responses to the mentioned covariates. The relatively small sample sizes and high variation in counts for each species impeded us from investigating single species abundance responses. Instead, we transformed the response variable into presence/absence to investigate single species occurrence probability in relation to the different covariates, using a GLM with binomial distribution and *logit* function.

Before fitting models, we checked that none of the continuous covariates were highly correlated. We standardized all variables to a mean of zero and one unit of standard deviation for analysis. For each modeling procedure, we fit all model combinations with all covariates. We used Akaike's Information Criterion corrected for small sample sizes (AICc) to perform model selection (Burnham and Anderson, 2002). We selected the most parsimonious models based on a $\Delta AICc < 2$ and model averaged results to calculate parameter estimates and 95% confidence intervals (CI; Burnham and Anderson, 2002), using the *MuMIn* and *AICcmodavg* packages in R (R Development Core Team, 2016).

Results

Among wild species, wild boars were the most abundant (46.9%), followed by nilgai (25.7%), chital (18.8%), barking deer (5.7%) and sambar (2.8%; Table 1). The most abundant livestock type was cattle (54.9%), followed by goats (24.9%), buffalo (17.0%), and sheep (3.0%; Table 1). Livestock relative abundance was 6.2 times higher than all wild species combined (livestock = 20.71 ind/km vs wild species = 3.34 ind/km).

Ungulate ensemble abundances

The two most parsimonious models explaining ungulate assemblage abundance accounted for 100% of cumulative weight and included all four covariates (elevation, distance to roads, distance to agriculture, and livestock relative abundance (Table 2, Table A1)). Model averaged results indicated that the ungulate assemblage abundance increased with increasing elevation (0.41 [95% CI: 0.27 - 0.54]) and increasing distance from roads (0.20 [95% CI: 0.02 - 0.39]), but decreased with increasing distance from agricultural areas (-0.43 [95% CI: -0.65 - 0.21]) and increasing relative livestock abundance (-1.42 [95% CI: -2.07 - 0.78]) (Fig. 2). All variables were significant (confidence intervals did not overlap 0).

Ungulate single-species occurrence

The six most parsimonious models that best explained chital presence accounted for 93% cumulative model weight and included the four covariates (elevation, distance to roads, distance to agriculture and livestock relative abundance; Table 3, Table A2). We found two models that best explained the presence of wild boar, which together accounted for 60% of the model weight and included three covariates (elevation, distance to roads, and livestock relative abundance; Table 3). Four models best explained sambar's presence and accounted for 55% model weight. For this species, however, the null model was the most parsimonious model, suggesting a lack of explanatory power (Table 3). This is due to the small number of detections (n = 5) for this species (Table 1). For nilgai, three models best explained its presence probability, which accounted for 49% of the model weight and included elevation and livestock relative abundance (Table 3). Finally, the nine most parsimonious models that best explained the presence of barking deer accounted for 78% of the model weight and included all four covariates (Table 3).

Elevation was the most important covariate explaining the presence probability of all five ungulates, with presence probability increasing with increasing elevation (Fig. 3, Fig. 4). Distance to the nearest road was negatively related to the presence of chital, positively related to the presence of wild boar, and slightly negatively related to the presence of barking deer (Fig. 3). Chital presence was slightly negatively associated with the distance to the nearest agricultural area, whereas sambar and barking deer presence probability varied little with changes in distance to the nearest agricultural area (Fig. 3). Finally, all five species' presence probability was negatively associated with increasing livestock relative abundance (Fig. 3). This relationship was much stronger for chital and wild boar, but with little change for the other three species (Fig. 4). In all these trends, 95% confidence intervals overlapped zero.

Discussion

In this study, we found livestock abundance outnumbered wild species abundance by 6:1 in the community managed forests of Nepal. The overall abundance of the five wild ungulate species was negatively related to livestock abundance and positively related to elevation. Similarly, all five species of wild ungulates occurred mainly in elevated areas (> 300m) dominated by Sal forests, mixed type forest (forests mostly dominated by *Terminalia alata*, *Adina cordifolia, Schima wallichii* and *Dalbergia sissoo*), and overall fewer human disturbances in comparison to the lowland forests. Results suggest that livestock, which occur predominantly on lowlands (93% of livestock < 300 m.a.s.l.), are excluding wild herbivores, which in turn occur mainly on highlands (69% of ungulates > 300 m.a.s.l.). More data are certainly needed to identify significant effects on large-herbivore occurrence at the single species level. However, the effect of livestock on the community

abundance and the trends we report on single species are largely informative for a system that is rapidly losing forest cover and that needs urgent action to protect critical habitat.

The chital is one of the most abundant deer species in Nepal (Bhattarai & Kindlmann, 2013; Thapa & Kelly, 2017). However, the distribution of this species is almost entirely restricted to protected areas (Wegge et al., 2009; Bhattarai & Kindlmann, 2013). Our finding of 0.59 individual/km is significantly lower than reported for Nepal's protected areas. While our estimates are not directly comparable, previous research has reported abundances that are clearly much higher than our study area (84.7 ± 7.9 ind/km2, Wegge et al., 2009; 31.73 ± 4.26 ind/km2, Bhattarai & Kindlmann, 2012). We found that chital preferred elevated areas and areas with lower livestock abundance. Livestock higher abundance and anthropogenic activities in the lower elevated areas (< 300m) might explain chital preference towards elevated areas. Our result supported those from Bagchi et al. (2008), Wegge et al. (2009), who found that chital are using suboptimal habitats given high pressure from human related activities.

The wild boar is one of the most widely distributed species in Nepal, occurring from lowland (< 100 m) to the mid-hills (around 1500 m) (Pandey et al., 2016; Thapa & Kelly, 2017; Bhandari et al., 2019). Thus, our findings that wild boar was the most abundant wild species is not surprising. We also found that wild boar preferred elevated areas and avoided livestock and roads, similarly to findings by Ballari & Barrios-Garcia (2014). Many studies identified the wild boar as one of the major drivers of human-wildlife conflict in protected areas of Nepal (Pandey et al., 2016). However, based on our field observations (unpublished data), we did not find any crop damage by the wild boar. Furthermore, our results did not show a relationship between wild boar locations and agricultural land. Our results suggest that wild boars occur only in areas with low human impact, likely reinforced by hunting pressure (Ballari & Barrios-Garcia, 2014; Pandey et al., 2016).

The distribution of sambar in Nepal is mostly restricted to Parsa, Chitwan, Banke, and Bardia National Parks, and includes nearby habitats. The abundance and density of the sambar in the central lowland, such as Chitwan National Park and Bardia National Park, are comparatively higher than estimates from eastern (this study) and western Nepal (Suklaphanta National Park: Karki 2011). Sambar are highly sensitive to anthropogenic pressures (Wang, 2010; Yen et al., 2014; Simcharoen et al. 2014). Consequently, we found sambar to be the rarest species in our study (0.12 mean individual/km). In most parts of the country, this species prefers floodplains with grass and riverine forest (Wegge et al., 2009; Simcharoen et al., 2014). The lack of floodplains with abundant grass in the study area could also explain low sambar abundance.

Nilgai is endemic to the Indian subcontinent (Leslie, 2008). Nepal's lowland region represents a small population (< 400 individual) of nilgai which is sparsely distributed, mostly outside of Nepal's protected areas (Aryal, 2007; Baral, 2014; Khanal et al., 2018). We found nilgai to be the second most abundant species of our species surveyed. Its presence was positively associated with higher elevation and negatively associated with increasing livestock abundance. This species may be competing with livestock or alternatively, conflict with local farming communities because of crop damage may be pushing the species into the highlands where human impact is lower (Baral, 2014; Khanal et al., 2018). With most nilgai populations occurring outside protected areas, regulating human activities to ensure that wild ungulates can coexist with livestock will be critical for the future of this species.

We found lower numbers (0.19 mean individual/km) of barking deer than other wild ungulates. Barking deer is widely distributed in lowland Nepal and mid-hills (approximately up to 3000 m) (Karki, 2011; Paudel et al., 2015). We found that this species preferred the elevated landscape, and its presence probability decreased with increasing road distance, distance to agriculture, and number of livestock. Our results support the findings that barking deer prefer forested environments with low growing vegetation (Teng et al., 2004; Odden & Wegge, 2007; Paudel & Kindlmann, 2012). Barking deer is a solitary, forest-dwelling ruminant and inhabits dense shrub cover in the broad-leaved forests (Teng et al., 2004). Research conducted by Paudel and Kindlmann (2012) in western Nepal found that barking deer also preferred midhill areas. Teng et al. (2014) noted that barking deer are found in forest areas with mature trees with large canopies, tall shrubs, denser shrub cover, and/or areas for concealment. These habitat characteristics for the species make it possible that we have failed to detect the species when the species was present. Future research accounting for detection probability (MacKenzie et al., 2006), not just for this species, but for the entire community, will be important future steps to improve our results.

Implication for conservation

Wildlife conservation outside the protected area system of Nepal is challenging. Increases in human population are exacerbating pressures on natural resources, with concomitant increases in deforestation and habitat fragmentation (Halladay & Gilmour, 1995; DFRS, 2015; Shrestha et al., 2018). Results from our study suggest that high livestock abundance in the lowland forests are excluding ungulates, which occur mainly in elevated areas where livestock abundance is much lower. Conditions of these elevated areas, however, may be less favorable to sustain high population abundances and can compromise the population stability of these species. The high abundance of livestock in non-protected areas of Nepal may compromise the future presence of wild ungulates.

While more research is needed to confirm the trends found in this study, as our limited sample size makes it hard to generalize results on a wide scale, urgent management actions are needed to regulate the abundance of livestock in this human dominated landscape for the conservation of wild ungulate species. Declining wild ungulates in the natural environment can be the cause of human-carnivore conflict, with predators focusing on domesticated prey that have replaced wild species (Ramakrishnan et al., 1999; Xiao et al., 2018). This might not only affect ungulate distributions, but also alter prey-predator relationships (Ramakrishnan et al., 1999). Most of the community forests outside the protected areas systems have to be managed properly. Because our study site is connected to the Parsa National Park, it serves as an important biological corridor and potential habitat for many large predators. The conservation of wild ungulates is important to maintain natural predator-prey relationships, as well as to minimize human-wildlife conflict (Wegge et al., 2009; Allendorf et al., 2020; Bhandari et al., 2020).

In addition, protected landscapes in lowland Nepal have not been successful in supporting populations of many species in sharp decline, such as nilgai (Baral, 2014; Khanal et al., 2018) and sambar (Wegge et al., 2009). These species are known to be a major portion of the diet of charismatic species such as tiger and striped hyena (Bhandari et al., 2020). Extending protection outside formal protected areas boundaries, while also incorporating ecotourism opportunities, can be beneficial to the community in order to generate alternative income sources with minimum human-wildlife conflict. Management approaches with dual goals of regulating livestock grazing and improving habitat conditions for wild ungulates and other species, would be helpful for sustainable biodiversity conservation in the lowlands of Nepal.

Conclusion

In this study, we documented for the first time that high livestock abundances in the non-protected communal forests of Nepal are highly affecting the abundance and presence of many wild ungulates. The high livestock abundance found in the lowland forests appears to be explaining the presence of wild ungulates mainly on higher lands, thus, ungulates are being extirpated from the lowlands. These findings are important, not only for the large herbivores described here, but also for other critical endangered species that depend on these habitats for survival. With formal reserves across Nepal being insufficient to protect the space use needs of many large terrestrial animals, management strategies that favor the coexistence of wild ungulates with human activities is imperative for the future of wildlife.

Acknowledgments

We would like to thank the Katie Adamson Conservation Fund, US for funding the study. Some equipment was provided by Idea Wild, US. We thank the Department of Forestry, Babarmahal, Kathmandu, Nepal for granting study permission. Our thanks go to Umesh Pokhrel, Shambhu Bishwakarma, and Bishnu Thapa for helping during fieldwork. We thank the district forest offices in Rautahat and Bara for collaboration during fieldwork.

Authors' contributions :

Shivish Bhandari: Conceptualization-Lead, Data curation-Lead, Formal analysis-Supporting, Validation-Equal, Writing-original draft-Lead, Writing-review & editing-Equal.

Ramiro Crego: Formal analysis-Lead, Supervision-Equal, Validation-Equal, Visualization-Lead, Writing-original draft-Equal, Writing-review & editing-Lead.

Jared Stabach: Supervision-Lead, Validation-Equal, Visualization-Lead, Writing-original draft-Equal, Writing-review & editing-Lead.

Conflicts of interest/Competing interests : The authors declare that they have no conflict of interest.

Data Accessibility

Publisher: Dryad

https://doi.org/10.5061/dryad.jq2bvq87b

References

Acharya KP, Paudel PK, Neupane PR, Kohl M (2016) Human-wildlife conflicts in Nepal: patterns of human fatalities and injuries caused by large mammals. PLoS ONE 11(9): e0161717. https://doi.org/10.1371/journal.pone.0161717.

Allendorf TD, Gurung B, Poudel S, Dahal S and Thapa S (2020). Using community knowledge to identify potential hotspots of mammal diversity in southeastern Nepal. Biodivers Conserv 29:933–946. https://doi.org/10.1007/s10531-019-01919-0.

Aryal A (2007). Blue bull (*Boselaphus tragocamelus*) in Lumbani- A world heritage site of Nepal. TigerPaper 32: 4-9.

Atwood TB, Valentine SA, Hammill E, McCauley DJ, Madin EMP, Beard KH, Pearse WD (2020) Herbivores at the highest risk of extinction among mammals, birds, and reptiles. Sci Adv 6:eabb8458. https://doi.org/10.1126/sciadv.abb8458.

Aziz MA, Tollington S, Barlow A, Goodrich J, Shamsuddoha M, Islam MA, Groombridge JJ (2017) Investigating patterns of tiger and prey poaching in the Bangladesh Sundarbans: implications for improved management. Glob Ecol Conserv 9: 70–81. https://doi.org/10.1016/j.gecco.2016.12.001.

Bagchi S, Goyal SP, Shankar K (2008). Social organisation and population structure of ungulates in a dry tropical forest in western India (Mammalia, Artiodactyla). Mammalia 72: 44–49. https://doi.org/10.1515/MAMM.2008.008.

Ballari SA, Barrios-Garcia MN (2014) A review of wild boar Sus scrofa diet and factors affecting food selection in native and introduced ranges. Mammal Rev 44:124–134. https://doi.org/10.1111/mam.12015.

Baral HS (2014) Have protected areas failed to conserve Nilgai in Nepal? Gnusletter 32: 6-9.

Benitez-Lopez A, Alkemade B, Verweij PA (2010) The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. Biol Conserv 143: 1307-1316.https://doi.org/10.1016/j.biocon.2010.02.009.

Berger J (2004). The last mile: how to sustain long-distance migration in mammals. Conserv Biol 320–331. https://doi.org/10.1111/j.1523-1739.2004.00548.x.

Bhandari S, Chalise MK (2016) People's attitudes toward striped hyena (*Hyaena hyaena* Linnaeus, 1758) (Mammalia: carnivora: Hyaenidae) conservation in lowland Nepal. JoTT 8: 9125-9130. https://doi.org/10.11609/jott.2518.8.9.9125-9130.

Bhandari S, Mawhinney BA, Johnson D, Bhusal DR, Youlatos D (2019) Coexistence of humans and leopards in Shivapuri Nagarjun National Park, Nepal. Russ J Ecol 50: 590-592. https://doi.org/10.1134/S1067413619060031. Bhandari S, Morley C, Aryal C, Shrestha UB (2020) The diet of the striped hyena in Nepal's lowland regions. Ecol Evol 10: 7953-7962. https://doi.org/10.1002/ece3.6223.

Bhattarai BP, 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 57:89–97. https://doi.org/10.1007/s13364-011-0047-8.

Bhattarai BP, Kindlmann P (2013) Effect of human disturbance on the prey of tiger in the Chitwan National Park Implications for park management. J Environ Manage 131: 343-350.https://doi.org/10.1016/j.jenvman.2013.10.005.

Burnham KP, Anderson DR (2002) A practical information-theoretic approach. Model selection and multimodel inference, 2nd ed. Springer, New York.

Brook BW, Sodhi NS, Ng PKL (2003) Catastrophic extinctions follow deforestation in Singapore. Nature 424: 420–423.https://doi.org/10.1038/nature01795.

Cardillo M, Purvis A, Sechrest W, Gittleman JL, Bielby J, Mace GM (2004) Human population density and extinction risk in the world's carnivores. PLoS Biol 2(7):e197. https://doi.org/10.1371/journal.pbio.0020197.

Ceballos G, Ehrlich PR (2002) Mammal population losses and the extinction crisis. Science 296:904–907. https://doi.org/10.1126/science.1069349.

Ceballos G, Ehrlich PR, Dirzo R (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. PNAS 114: E6089-E6096.https://doi.org/10.1073/pnas.1704949114.

Ceballos G, Ehrlich PR, Raven PH (2020) Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. PNAS 117: 13596–13602. https://doi.org/10.1073/pnas.1922686117.

Chao S (2012) Forest peoples numbers across the worlds. Forest people program, UK. www.forestpeoples.org.

Craigie ID, Baillie JEM, Balmford A, Carbone C, Collen B, Green RE, Hutton JM (2010) Large mammal population declines in Africa's protected areas. Biol Conserv 143: 2221–2228.https://doi.org/10.1016/j.biocon.2010.06.007.

DFRS (2015) State of Nepal's Forests. Department of Forest Research and Survey. Kathmandu, Nepal.

DiMarco M, Boitani L, Mallon D, Hoffmann M, Iacucci A, Meijaard E, Visconti P, Schipper J, Rondinini C (2014). A retrospective evaluation of the global decline of carnivores and ungulates. Conserv Biol 28: 1109-1118. https://doi.org/10.1111/cobi.12249.

Farr TG, Rosen PA, Caro E, Crippen R, Duren R, Hensley S, Kobrick M, Paller M, Rodriguez E, Roth L, Seal D, Shaffer S, Shimada J, Umland J, Werner M, Oskin S, Burbank D, Alsdorf D (2007) The shuttle radar topography mission. Rev Geophys 45: RG2004. https://doi.org/10.1029/2005RG000183.

Halladay P, Gilmour DA (1995) Conserving biodiversity outside protected areas the role of traditional agroecosystems. IUCN Gland, Switzerland, and Cambridge, UK.https://portals.iucn.org/library.

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. Science 342: 850-853. https://doi.org/10.1126/science.1244693.

Hempson GP, Archibald S, Bond WJ (2017) The consequences of replacing wildlife with livestock in Africa. Sci Rep 7: 17196.https://doi.org/10.1038/s41598-017-17348-4.

Harris G, Thirgood S, Hopcraft JGC, Cromsigt JP, Berger J (2009) Global decline in aggregated migrations of large terrestrial mammals. Endanger Species Rese 7:55-76. https://doi.org/10.3354/esr00173.

IUCN (2020) International Union for Conservation of Nature (IUCN). https://www.iucn.org/.

Karki JB (2011) Occupancy and abundance of tigers and their prey in the Terai Arc Landscape, Nepal. Dissertation, Forest Research Institute University, India.

Kery M (2010) Introduction to WinBUGS for ecologists: A Bayesian approach to regression, ANOVA, mixed models and related analyses. Elsevier, Burlington, MA, USA.

Khadka KK (2017) Habitat ecology, trophic interactions, and distribution of endangered Himalayan musk deer in the Nepal Himalaya. Dissertation, University of Arkansas, USA.

Khanal S, Aryal A. Morley CG, Wright W and Singh NB (2018) Challenges of conserving Blue Bull (*Boselaphus tragocamelus*) outside the protected areas of Nepal. Proc Zool Soc 71: 352–362.https://doi.org/10.1007/s12595-017-0218-y.

Leslie DM (2008) Boselaphus tragocamelus (Artiodactyla: Bovidae). Mamm Species 813: 1–16.https://doi.org/10.1644/813.1.

Lutz W, Sanderson W, Scherbov S (1997) Doubling of world population unlikely. Nature 387: 803-805. https://doi.org/10.1038/42935.

Lutz W, Sanderson W, Scherbov S (2001) The end of world population growth. Nature 412:543-545. *https://doi.org/10.1038/35087589*.

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LA, Hines JE (2006) Occupancy modeling and estimation. Elsevier, San Diego, California, USA.

Mishra C, Wieren SEV, Ketner P, Heitkonig IM, Prins HHT (2004) Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. J Appl Ecol 41: 344–354. https://doi.org/10.1111/j.0021-8901.2004.00885.x.

Newmark WD (2008) Isolation of African protected areas. Front Ecol Environ 6: 321-328. https://doi.org/10.1890/070003.

Odden M, Wegge P (2007) Predicting spacing behavior and mating systems of solitary cervids: a study of hog deer and Indian muntjac. Zoology 110: 261-270.https://doi.org/10.1016/j.zool.2007.03.003.

Pandey P, Shaner PJL, Sharma HP (2016) The wild boar as a driver of human-wildlife conflict in the protected park lands of Nepal. Eur J Wildl Res 62: 103-108. https://doi.org/10.1007/s10344-015-0978-5.

Paudel PK, Hais M, Kindlmann P (2015) Habitat suitability models of mountain ungulates: identifying potential areas for conservation. Zool Stud 54:37. https://doi.org/10.1186/s40555-015-0116-9.

Paudel PK, Kindlmann P (2012) Human disturbance is a major determinant of wildlife distribution in Himalayan midhill landscapes of Nepal. Anim Conserv 15:283–293. https://doi.org/10.1111/j.1469-1795.2011.00514.x.

Poffenberger M (2006) People in the forest: community forestry experiences from Southeast Asia. IJESD 5:57 - 69. https://doi.org/10.1504/IJESD.2006.008683.

QGIS Development Team (2009) QGIS geographic information system. open source geospatial foundation project.http://qgis.osgeo.org.

Ramakrishnan U, Coss RG, Pelkey NW (1999) Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. Biol Conserv 89: 113-120.https://doi.org/10.1016/S0006-3207(98)00159-1.

R Development Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ripple et al (2016) Saving the world's terrestrial megafauna. BioScience 66: 807-812.https://doi.org/10.1093/biosci/biw092.

Roman-Palacios C, Wiens JJ (2020) Recent responses to climate change reveal the drivers of species extinction and survival. PNAS 117: 4211–4217. https://doi.org/10.1073/pnas.1913007117.

Schipper et al (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. Science 322: 225-230. https://doi.org/10.1126/science.1165115.

Shrestha S, Shrestha UB, Bawa K (2018) Socio-economic factors and management regimes as drivers of tree cover change in Nepal. PeerJ 6:e4855.https://doi.org/10.7717/peerj.4855.

Shrestha UB, KS. Bawa (2013) Trade, harvest, and conservation of Caterpillar fungus (*Ophiocordyceps sinensis*) in the Himalayas. Biol Conserv 159: 514 – 520.https://doi.org/10.1016/j.biocon.2012.10.032.

Simcharoen A, Savini T, Gale GA, Roche E, Chimchome V, Smith JLD (2014) Ecological factors that influence sambar (*Rusa unicolor*) distribution and abundance in western Thailand: implications for tiger conservation. Raffles Bull Zool 62:100-106.

Smith, JLD, Mishra HR (1992) Status and distribution of Asian elephants in central Nepal. Oryx 26: 34-38. https://doi.org/10.1017/S0030605300023206.

Smith JLD, Ahearn SC, McDougal C (1998) Landscape analysis of tiger distribution and habitat quality in Nepal. Conserv Biol 12: 1338–1346. https://doi.org/10.1111/j.1523-1739.1998.97068.x.

Sodhi NS, Koh LP, Brook BW, Ng PKL (2004) Southeast Asian biodiversity: An impending disaster. Trends Ecol Evol 19: 654–660. https://doi.org/10.1016/j.tree.2004.09.006.

Sodhi NS, Koh LP, Clements R, Wanger TC, Hill JK, Hamer KC, Clough Y, Tscharntke T, Posa MRC, Lee TM (2010) Conserving southeast Asian forest biodiversity in human-modified landscapes. Biol Conserv 143: 2375–2384. https://doi.org/10.1016/j.biocon.2009.12.029.

Squires D (2014) Biodiversity conservation in Asia. Asia & the Pacific Policy Studies 1: 144-159. https://doi.org/10.1002/app5.13.

Teng L, Liu Z, Song YL, Zeng Z (2004). Forage and bed sites characteristics of Indian muntjac (*Muntiacus muntjak*) in Hainan Island, China. Ecol Res 19: 675–681. https://doi.org/10.1111/j.1440-1703.2004.00683.x.

Thapa K, Kelly M (2017) Prey and tigers on the forgotten trail: high prey occupancy and tiger habitat use reveal the importance of the understudied Churia habitat of Nepal. Biodivers Conserv 26:593–616. https://doi.org/10.1007/s10531-016-1260-1.

Veldhuis et al (2019) Cross-boundary human impacts compromise the Serengeti-Mara ecosystem. Science 363:1424-1428. https://doi.org/10.1126/science.aav0564.

Wang SW (2010) Estimating population densities and biomass of ungulates in the temperate ecosystem of Bhutan. Oryx 44: 376–382.https://doi.org/10.1017/S0030605310000487.

Weggee P, Odden M, Pokharel CP, Storaas T (2009) Predator-prey relationship and responses of ungulates and their predators to the establishment of protected areas: a case study of tigers, leopards and their prey in Bardia National Park, Nepal. Biol Conserv 142: 189–202.https://doi.org/10.1016/j.biocon.2008.10.020.

Western D, Russell S, Cuthill I (2009) The status of wildlife in protected areas compared to non-protected areas of Kenya. PLoS ONE 4(7): e6140. https://doi.org/10.1371/journal.pone.0006140.

Wittemyer G, Elsen P, Bean WT, Burton AC, Brashares JS (2008) Accelerated human population growth at protected area edges. Science 321:123-126. https://doi.org/10.1126/science.1158900.

Woodroffe R, Ginsberg JR (1998) Edge effects and the extinction of populations inside protected areas. Science 280:2126–2128. https://doi.org/10.1126/science.280.5372.2126.

Xiao W, Hebblewhite M, Robinson H, Feng L, Zhou B, Mou P, Wang T, Ge J (2018) Relationships between humans and ungulate prey shape Amur tiger occurrence in a core protected area along the Sino-Russian border. Ecol Evol 8:11677-11693. https://doi.org/10.1002/ece3.4620.

Xu H, Tang X, Liu J, Ding H, Wu J, Zhang M, Yang Q, Cai L, Zhao H, Liu Y. (2009) China's progress toward the significant reduction of the rate of biodiversity loss. BioScience 59:843-852.https://doi.org/10.1525/bio.2009.59.10.6.

Yen SC, Yang Y, Ou HY (2014) Habitat of the vulnerable formosan sambar deer Rusa unicolor swinhoii in Taiwan. Oryx 48: 232–240.https://doi.org/10.1017/S0030605312001378.

Legends to the tables

Table 1. Wild and domestic species animal counts and prevalence at 35 transects across the study area in Nepal.

	Total number of animals	Mean ind/km $(+-SE)$	Prevalence $(\%)$
Wild species			
Chital	33	0.59(0.21)	34.29
Wild boar	82	1.54(0.45)	42.86
Sambar	5	0.12(0.06)	11.43
Nilgai	45	0.90(0.37)	28.57
Barking deer	10	0.19(0.09)	20.00
Total	175	3.34(0.92)	54.28
Livestock			
Goat	271	5.30(2.23)	42.86
Sheep	33	0.91(0.66)	20.00
Cattle	597	10.48 (3.66)	65.71
Buffalo	185	4.02 (2.06)	11.43
Total	1086	20.71 (6.00)	74.29

Table 2. Table 2. Model selection results to investigate ungulate assemblage abundances in relation to elevation (m), distance to road (km), distance to agricultural fields (km) and livestock relative abundance (ind/km), in Nepal. Only the most parsimonious models are presented, i.e. $\Delta AICc < 2$. K = number of estimated parameters; AICc = Akaike's Information Criterion corrected for small samples; $\Delta AICc =$ difference in AICc, W = model weight, and Cum. W. = cumulative model weight.

Model	Κ	AICc	$\Delta AICc$	W	Cum. W
$\overline{\text{Elev} + \text{Dist. Road} + \text{Dist. Agr} + \text{Liv. Abund.}}$	5	296.6	0.00	0.71	0.71
Elev + Dist. Agr + Liv. Abund.	4	298.4	1.76	0.29	1

Table 3. Table 3. Model selection results to investigate five species of ungulate occurrence in Nepal. Only the most parsimonious models are presented, i.e. $\Delta AICc < 2$. The explanatory variables are elevation (m), distance to road (km), distance to agricultural fields (km), and livestock relative abundance. K = number of estimated parameters; AICc = Akaike's Information Criterion corrected for small samples; $\Delta AICc =$ differences in AICc, W = model weight, and Cum. W. = cumulative model weight.

Species	Model	Κ	AICc	$\Delta AICc$	W	Cum. W
Chital	Elev + Dist. Road	3	29.85	0.00	0.20	0.20
	Elev + Dist. Road + Dist. Agr	4	29.95	0.10	0.19	0.39
	Elev + Dist. Road + Dist. Agr. + Liv. Abund.	5	30.31	0.46	0.16	0.54
	Elev + Liv. Abund.	3	30.60	0.75	0.14	0.68
	Elev + Dist. Road + Liv. Abund.	4	30.68	0.83	0.13	0.81
	Elev + Dist. Agr. + Liv. Abund.	4	30.85	1.00	0.12	0.93
Wild boar	Elev + Liv. Abund.	3	38.45	0.00	0.42	0.42
	Elev + Dist. Road + Liv. Abund.	4	40.26	1.81	0.17	0.59
Sambar	Null model	1	27.00	0.00	0.19	0.19
	Elev	2	27.30	0.30	0.17	0.36
	Liv. Abund.	2	28.12	1.13	0.11	0.47
	Dist. Agr	2	28.76	1.76	0.08	0.55
Nilgai	Elev	2	42.47	0.00	0.26	0.26
	Null model	1	44.00	1.53	0.12	0.38
	Elev + Liv. Abund.	3	44.15	1.68	0.11	0.49
Barking deer	Elev	2	35.85	0.00	0.15	0.15
	Elev + Dist. Road	3	36.11	0.26	0.13	0.28
	Elev + Dist. Agr	3	37.05	1.20	0.08	0.36
	Elev + Liv. Abund.	3	37.08	1.23	0.08	0.44
	Null model	1	37.15	1.30	0.08	0.51
	Elev + Dist. Road + Dist. Agr.	4	37.28	1.43	0.07	0.58
	Liv. Abund.	2	37.36	1.52	0.07	0.65
	Dist. Agr.	2	37.45	1.60	0.07	0.72
	Dist. Agr $+$ Liv. Abund.	3	37.58	1.73	0.06	0.78



Ĩ.
Ξ.
rel
Q.
ĝ.
2
ß
)a1
ġ.
M
-5
T.C.
8
ě
g
ee
-
10
8
ha
p.
an
÷.
-E
del.
pr
6
his
Ē
00
61
19
68
3.6
43(
80
<u>66</u>
15
Ш.,
-8
Ŧ.
22
2
Ξ.
20
ę.
.s
E
P-
<u></u>
8
ē
t P
out p
thout p
without p
se without p
suse without p
reuse without p
No reuse without p
l. No reuse without p
ved. No reuse without p
erved. No reuse without p
eserved. No reuse without p
s reserved. No reuse without p
thts reserved. No reuse without p
rights reserved. No reuse without p
Il rights reserved. No reuse without p
All rights reserved. No reuse without p
er. All rights reserved. No reuse without p
nder. All rights reserved. No reuse without p
funder. All rights reserved. No reuse without p
w/funder. All rights reserved. No reuse without p
hor/funder. All rights reserved. No reuse without p
withor/funder. All rights reserved. No reuse without p
e author/funder. All rights reserved. No reuse without p
the author/funder. All rights reserved. No reuse without p
is the author/funder. All rights reserved. No reuse without p
er is the author/funder. All rights reserved. No reuse without p
lder is the author/funder. All rights reserved. No reuse without p
holder is the author/funder. All rights reserved. No reuse without p
ht holder is the author/funder. All rights reserved. No reuse without p
ight holder is the author/funder. All rights reserved. No reuse without p
wright holder is the author/funder. All rights reserved. No reuse without p
opyright holder is the author/funder. All rights reserved. No reuse without p
e copyright holder is the author/funder. All rights reserved. No reuse without p
The copyright holder is the author/funder. All rights reserved. No reuse without p
- The copyright holder is the author/funder. All rights reserved. No reuse without p
- The copyright holder is the author/funder. All rights reserved. No reuse without p
20 - The copyright holder is the author/funder. All rights reserved. No reuse without p
2020 - The copyright holder is the author/funder. All rights reserved. No reuse without p
p $2020-$ The copyright holder is the author/funder. All rights reserved. No reuse without p
Sep $2020 - $ The copyright holder is the author/funder. All rights reserved. No reuse without p
1 Sep $2020 - $ The copyright holder is the author/funder. All rights reserved. No reuse without p
$\scriptstyle 11$ Sep 2020 — The copyright holder is the author/funder. All rights reserved. No reuse without p
tea 11 Sep $2020 - $ The copyright holder is the author/funder. All rights reserved. No reuse without p
horea 11 Sep $2020 -$ The copyright holder is the author/funder. All rights reserved. No reuse without p
uthorea 11 Sep $2020 - $ The copyright holder is the author/funder. All rights reserved. No reuse without p
Authorea 11 Sep $2020 - $ The copyright holder is the author/funder. All rights reserved. No reuse without p
on Authorea 11 Sep $2020 - $ The copyright holder is the author/funder. All rights reserved. No reuse without p
sd on Authorea 11 Sep $2020 - $ The copyright holder is the author/funder. All rights reserved. No reuse without p



