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Habitat suitability models of mountain ungulates: identifying potential areas for conservation

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Abstract

Background: Determining the distribution of species and of suitable habitats is a fundamental part of conservation planning. We used slope and ruggedness of the terrain, forest type and distance to the nearest village to construct habitat suitability maps for three mountain ungulates (barking deer (*Muntiacus muntjak*), Himalayan goral (*Naemorhedus goral*) and Himalayan serow (*Capricornis thar*)) in the midhills of western Nepal. We used locations of sightings and signs of presence of these mountain ungulates collected during surveys along transect to derive a suitability value for each variable using Jacob's index. A multiplication approach was used to combine environmental variables and produce a habitat suitability map for each of the three species. An independent dataset was used to evaluate the maps using Boyce's index. This approach provides an overview of the probable distributions of the species in question.

Results: We predict that of the total area studied, 57% is suitable for *M. muntjak*, 67% for *N. goral* and 41% for *C. thar.* Although there are suitable habitats for all three species throughout the study area, the availability of high-quality habitats for these species varied considerably.

Conclusions: Suitable habitats for *N. goral* and *C. thar* were fragmented and mostly confined to the southern and northern parts of the study area. This study provides important baseline information for conservation biologists concerned with maintaining biodiversity in the midhills of Nepal.

Keywords: Capricornis thar; Habitat model; Midhills; Muntiacus muntjak; Naemorhedus goral; Nepal

Background

Human interference in the last remaining wilderness areas has resulted in a drastic decline in population size and distribution range of many species of wildlife (Mills 2009; Paudel and Kindlmann 2012a; Morrison et al. 2012). However, actions aimed to minimize this effect are often launched too late, usually after species and their habitats have already been seriously affected (Mittermeier et al. 1998; Myers et al. 2000; Brooks et al. 2002). Hence, it is important to maintain critical wildlife habitats (Poiani et al. 2000; Sala et al. 2000) and establish what determines the present distribution of species, which is especially difficult in mountainous areas and when species population density is low (Gibson et al. 2004). Generally, large-scale

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The midhills in Nepal are an intermediary landscape between low-lying Tarai in the south and Himalayan region in the north. This region harbours the highest species diversity in the country (Paudel et al. 2012; Primack et al. 2013). However, ecosystems in the midhills were poorly studied in the past; therefore, there is almost no information on their biodiversity and consequently they are very poorly represented in the protected area network (Hunter and Yonzon 1993; Paudel et al. 2012; Paudel and Heinen 2015). The midhills are densely populated and the forest areas there are highly fragmented due to human exploitation for firewood, fodder and



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timber including agricultural lands (Paudel and Šipoš 2014). Subsistence hunting, detrimental to wildlife, is also widespread here (Jackson 1979; Paudel 2012; Paudel and Kindlmann 2012a). Such activities in fragmented forests adversely affect the community structure of wildlife (Andrén 1994; Peres 2001; Fahrig 2003; Paudel and Kindlmann 2012a). For example, Himalayan tahr (Hemitragus jemlahicus), which was once common in the midhills of Nepal, is now extinct there because of habitat loss and hunting (Green 1979), and Himalayan serow (Capricornis thar) is confined to remote forest areas on the slopes of mountains (Wegge and Oli 1997; Paudel and Kindlmann 2012b). The same is true for many other wildlife species living in the midhills. Because of the remoteness and inaccessibility, the distributions of most species in this region are unknown.

Two broad approaches - (1) expert opinion integrated into GIS and (2) mathematical and machine learning algorithms (e.g. tree-based classification, neural networks and random forest, ecological niche factor analysis) - are used to produce habitat suitability maps (Pearce and Ferrier 2000; Guisan and Zimmermann 2000; Store and Kangas Store and Kangas 2001; Breiman 2001; Yamada et al. 2003). Expert opinion has been used with GIS modelling techniques to provide a basis for developing habitat suitability model when adequate empirical data are not available (Store and Kangas Store and Kangas 2001; Yamada et al. 2003; see details in Thuiller and Münkemüller 2010). There is some uncertainty regarding the reliability of such methods mainly because of potential errors in the expert judgments (Maddock and Samways 2000). Similarly, it is possible to use robust statistical approaches to produce habitat suitability maps (e.g. MADIFA, ENFA and BIOMOD) (Guisan and Zimmermann 2000; Hirzel et al. 2002; Rushton et al. 2004; Thuiller and Münkemüller 2010). Such approaches require advanced statistical and computing knowledge and a large dataset on environment collected using a stratified survey (Austin and Meyers 1996). Prior knowledge of environmental determinants of species distribution is crucial to improve the quality and reliability of predictions (Hirzel and Le Lay 2008). There is therefore a need for an alternative modelling approach that does not require sophisticated tools and can be implemented using limited environmental data based on documented species-habitat associations (Gavashelishvili and Lukarevskiy 2008). A multiplicative operation for combining important environmental variables is one of the widely used techniques of model construction (e.g. Liu et al. 2001; Dayton and Fitzgerald 2006).

This study aimed to produce habitat suitability maps for three mountain ungulates, still relatively common in the Nepalese midhills (barking deer (*Muntiacus muntjak*), Himalayan goral (*Naemorhedus goral*) and Himalayan serow (*Capricornis thar*)) and verify their accuracy. All of these ungulates are widely distributed across the Himalayan landscapes, but they exhibit distinct habitat affinities (see the 'Methods' section for details of the species studied). These maps have important applications not only for the conservation of these species, but also because these species serve as indicator species of healthy mountain ecosystem and form a part of the diet of endangered predators in the region: common and clouded leopard at low and snow leopard at high altitudes.

Methods

Study area

The study area (81°17′30.216″ to 82°42′58.158″ E, 28°28′ 57.261″ to 29°14′11.418″ N) comprises approximately 2,844 km² in the midhills of Western Nepal, situated between the Bardia National Park in the lowland Tarai and the Shey Phoksundo National Park in the mountain region (Figure 1).

The habitats vary from dense subtropical deciduous sal forest (Shorea robusta) in the south to alpine pastures in the north. The study area spans over five ecoregions: Himalayan subtropical broadleaf forest, endangered western Himalayan broadleaf forest (Olson et al. 2001), Himalayan subtropical pine forest, western Himalayan subalpine coniferous forest and western Himalayan alpine shrub and meadow (Wikramanayake 2002). The areas below 1,000 m, with a tropical climate, are dominated by sal (Shorea robusta) forest. Areas at altitudes of 1,000 to 2,000 m, with a subtropical climate, are dominated by chir pine (Pinus roxburghii) with an admixture of Quercus incana, Quercus lamellosa, Rhododendron arboreum, Alnus nepalensis etc. Areas at altitudes of 2,000 to 3,000 m, with a temperate climate, are dominated by oak, rhododendron and laurel stands along with conifers such as blue pine, fir and hemlock. In the subalpine zone (3,000 to 4,000 m), several conifers (Pinus wallichiana, Abies spectabilis, Abies pindrow, Tsuga dumosa) and broad-leaved species (Betula utilis, rhododendrons and Quercus semecarpifolia) form diverse types of vegetation (Paudel et al. 2012). In the alpine zone, above 4,000 m, there are some shrubs, but grassland is more common. The region also supports a high faunal (especially mammal) diversity, including 7% of the mammals endemic to this region (Paudel et al. 2012; Primack et al. 2013). Summer monsoon (June-September) accounts for about 80% of the precipitation and winter rain is infrequent (Das 1968).

Subsistence agriculture, supporting not much more than the people's basic survival, is the main occupation. Because of rapid population growth and expansion of the road network, human activities are putting an ever increasing pressure on the forests and the species living there (Paudel 2012).



Species studied

Barking deer is a relatively small and solitary cervid, which is widely distributed throughout large parts of Southeast Asia (Ohtaishi and Gao 1990; Prater 1990; Roberts 1999). It prefers dense forest with a high understory (Teng et al. 2004; Odden and Wegge 2007) but is also found in degraded forest areas near human settlements (Oka 1998). Because it is territorial, large concentrations of individuals of this species are rarely seen (Odden and Wegge 2007). Barking deer prefers plains and gentle slopes, but such areas have been degraded over the years. Their inability to live in the open and on rugged mountain slopes is limiting them to areas around human settlements (Paudel and Kindlmann 2012a).

Himalayan goral is associated with a wide variety of habitats throughout the mountains (Green 1987; Wegge and Oli 1997). It prefers open plant communities with good grass cover and avoids shrub-rich patches (Cavallini 1992), feeds primarily on grass in all seasons (Mishra and Johnsingh 1996; Fakhar-I-Abbas et al. 2008) and is adapted to steep and rugged mountain terrain (Green 1987; Cavallini 1992; Roberts 1999; Paudel and Kindlmann 2012a). Thus, the steep slope is an important feature preferred by goral (Cavallini 1992; Mishra and Johnsingh 1996; Paudel and Kindlmann 2012a).

Himalayan serow is an IUCN's near threatened (NT) mountain ungulate. It was widely distributed in the mountains of Himalaya (eastern part of the river Jamuna in Bangladesh, northern India, Tibet and Nepal). Now, it is very rare and confined to a few scattered, isolated populations in its former ranges (Green 1987; Grubb 2005) because of habitat loss and hunting (Prater 1990; Paudel and Kindlmann 2012a). In Nepal, the exact

distribution of serow is unknown and is restricted to steep forested hills and cliffs, in areas relatively inaccessible to the humans and in protected areas (Wegge and Oli 1997; Paudel and Kindlmann 2012a). Serow inhabits rugged mountains or ridges covered with thick bushes or forests (Nowak and Wilson 1999).

Species distribution data

We collected presence data for these three mountain ungulates by means of surveys along transects in 21 'clusters' in 2008, 2009 and 2010 (December-June), which were selected as follows: First, we superimposed a $1 \text{ km} \times 1 \text{ km}$ grid on the map of the study area using ArcMap 9.2[©] Geographic Information System. Then, we excluded pixels with less than 50% forest cover, which yielded a set of pixels shown in Figure 1. We generated random points with an 'inhibition distance' (i.e. the smallest distance allowed between any two random placed points) of 5 km. This procedure gave us 24 random points (hereafter 'cluster'). Among them, three points occurred in human habitation and therefore they were excluded. Around each of these 21 clusters, we laid out 10 to 20 transects (depending on its size) at least 100 m from the edge of a forest. We maintained at least 100-m distance between two transects based on the accessibility and availability of the forests. The transects included riversides and plains, ravines, mountain ridges and steep cliffs.

In each transect, the presence of species was assessed on the basis of the presence or absence of footprints and faeces within a circular plot with a radius of 2.5 m and by direct sighting at 100-m intervals along the transect, henceforth referred to as 'sampling points'. Two people, mostly local people acquainted with the forests, were involved in searching for signs of the presence of the species in question at each sampling point. Since sampling points were relatively small (approximately 20 m²), we searched carefully for signs of presence (footprints and faeces), and it is likely that all such signs were detected. If the animal is observed during searching of presence signs, we counted a corresponding sampling point as present. Here, we should be cautious that the absence site could be a pseudo-absence one. This will not affect our results because we are predicting the relative probability of occurrence of the species and the absences are interpreted as unused sites. In order to avoid confusing signs of the presence of livestock (e.g. sheep and goats) with those of wild herbivores, we tested our ability to distinguish footprints and faeces of barking deer, Himalayan goral and Himalayan serow from those of livestock. This test indicated that we were able to distinguish between the signs left by the three ungulates and livestock. Surveys were carried out at 4,328 sampling points along 432.8 km of transects, which varied in length from 0.3 to 2.5 km depending on the steepness of the terrain and vegetation. These surveys revealed a total of 687 signs of presence: 229 of barking deer, 316 of Himalayan goral and 142 of Himalayan serow. At each sampling point, we determined (1) vegetation type, elevation and (2) slope (Table 1). Other explanatory data (e.g. distance to the nearest village, topographic ruggedness; see Table 1 for details) were derived from the GIS.

Environmental variables

Based on documented species-habitat associations (Green 1987; Prater 1990; Cavallini 1992; Mishra and Johnsingh 1996; Wegge and Oli 1997; Roberts 1999; Grubb 2005; Odden and Wegge 2007; Paudel and Kindlmann 2012b; Paudel and Kindlmann 2012a), our field experience and models developed for similar species (Kushwaha et al. 2000), we used various numbers of categories of four main environmental variables (Table 1): We selected environmental variables describing landscape (i.e. slope, topographic ruggedness), habitat type (i.e. vegetation) and human influences (i.e. distance to the nearest village) based on the documented habitat affinities. We tested the performance of these environmental variables for predicting species presence using logistic regressions (Menard 2001). Before performing the regression analyses, we tested for multicollinearity among the data using a Pearson correlation matrix, because environmental variables that are correlated (r > 0.7) can bias a model (Berry and Feldman 1985). Nagelkerke R^2 and receiver operating characteristic curves (ROC) or area under curve (AUC) were used to evaluate the association of the habitat variables with the presence of species. ROC is a plot of true positive cases (or sensitivity) on the y-axis against corresponding false positive cases (or specificity)

on the *x*-axis for a range of threshold values (Fielding and Bell 1997). It provides a measure of discrimination ability, which varies from 0.5, when it is no better than expected on the basis of random choice, to 1.0, when it is perfectly discriminatory. Our results indicated that the environmental variables we selected had a high discriminatory ability (Table 2).

We classified environmental variables into a number of classes. Such classes are important when associations between species and environmental variables are nonlinear. Class boundaries here are based on ecological requirement of species in question or types of data:

- (i) slope (6 categories, spanning 15° each: 0 to 15, 15 to 30, ..., 75 to 90),
- (ii) topographic ruggedness (categorized into four classes using natural breaks based upon Jenks optimization: 0 to 0.05, 0.05 to 0.19, 0.19 to 0.44 and 0.44 to 0.99 see below for how these values were derived),
- (iii) forest type (11 classes of forests and 2 classes of land type: bushy areas and alpine meadow), and
- (iv) distance to the nearest village (less than 250, 500, 750, and 1,000 m and greater than 1,000 m)

The environmental data used here were the presence/ absence data, collected in 2008 and 2009 along 325.8 km of transects (76% of total 432.8 km) for model development (see below about the model: 'Preparation and evaluation of the suitability map'). This dataset was used to estimate relative probability of usage of the different categories of habitat based on four environmental variables. The remaining presence records, approximately 24% of the transect data, collected along 102 km of transects (collected in 2010), were used to evaluate the above model (see 'Preparation and evaluation of the suitability map').

Two Landsat ETM scenes taken on 25 December 2001 (path 143, row 40) and on 21 February 2003 (path 144, row 40), when there was no cloud cover, were obtained from the http://glovis.usgs.gov web pages. Both scenes were geometrically corrected. The data were classified using supervised classification (maximum likelihood -Geomatica 2005) based on 146 training areas (polygons), which included 11 vegetation and two land use units (see Table 1). The geographic coordinates of the training areas were determined in the field, using GPS mapping. As some types of vegetation have identical spectra (e.g. grassland vs. alpine meadow; lower temperate broad-leaved forest vs. temperate broad-leaved forest), it was not possible to distinguish between them so they were either aggregated or when possible separated on the basis of altitude (Digital Elevation Model). We separated types of vegetation on the basis of altitude only when they do not overlap

Table 1 Description of environmental variables used to produce the suitability maps

Variable	Description
Slope	
0 to 15	Slope of the land surface relative to the horizontal
15 to 30	measured in degrees
30 to 45	
45 to 60	
60 to 75	
75 to 90	
Ruggedness	
0 to 0.05	Topographic ruggedness measured in terms of
0.05 to 0.19	et al. 2007)
0.19 to 0.44	
0.44 to 0.99	
Forest type	
STSF	Subtropical sal forest: north tropical dry deciduous forest (Champion and Seth 1968), sub-tropical hill sal forest (Stainton 1972), hill sal forest (TISC 2002); altitudinal range: 300 to 1,000 m
SPF	Subtropical pine forest: chir pine forest (TISC 2002), sub-tropical pine forest (Champion and Seth 1968); altitudinal range: 1,000 to 2,000 m
STPBLF	<i>Subtropical pine broad-leaved forest</i> : chir pine broad-leaved forest (TISC 2002); altitudinal range: 1,000 to 2,000 m
UTCF	<i>Upper temperate blue pine forest:</i> (TISC 2002); altitudinal range: 2,500 to 3,000 m
RARA	<i>Grass and rocky areas</i> : barren hillsides devoid of trees because of rocks, frequently with dense forest nearby; altitudinal range: 300 to 3,200 m
TMF	<i>Temperate mixed forest</i> : fir-hemlock-oak forest (TISC 2002), fir-oak-rhododendron forest (TISC 2002), mixed blue pine-oak forest (TISC 2002); altitudinal range: 2,000 to 3,000 m
LTBLF	<i>Lower temperate broad-leaved forest:</i> lower temperate oak forest (TISC 2002), <i>Alnus</i> woods (Stainton 1972); altitudinal range: 2,000 to 2,500 m
TBLF	<i>Temperate broad-leaved forest</i> : oak-rhododendron forest (TISC 2002), rhododendron forest (TISC 2002), temperate mixed broad-leaved forest (Stainton 1972)
SABLF	<i>Subalpine broad-leaved forest:</i> birch-rhododendron forest (TISC 2002), subalpine mountain oak forest (TISC 2002), <i>Quercus semecarpifolia</i> forest (Stainton 1972; Champion and Seth 1968); altitudinal range: 3,000 to 4,000 m
SAMF	<i>Subalpine mixed forest</i> : fir-oak-rhododendron forest (TISC 2002), fir-hemlock-oak forest (TISC 2002); altitudinal range: 3,000 to 4,000 m
SACF	Subalpine conifer forest: fir forest (TISC 2002), Abies spectabilis forest (Stainton 1972), Abies pindrow forest (Stainton 1972); altitudinal range: 3,000 to 4,000 m
ВА	<i>Bushy area:</i> forest area covered with bushes; altitudinal range: 300 to 4.000 m

Table 1 Description of environmental variables used to produce the suitability maps (Continued)

AM	Alpine meadow: altitudinal range: >3,500 m
Distance to the nearest village	
250	Forest within a 250-m radius of the nearest village
500	Forest within a 500-m radius of the nearest village
750	Forest within a 750-m radius of the nearest village
1,000	Forest within a 1,000-m radius of the nearest village
>1,000	Forest outside a 1,000-m radius of the nearest village

in their altitudinal ranges. The resulting data were filtered (SIEVE) in order to remove disjointed single pixels. The accuracy of this classification was evaluated using the data (783 points) that were not used in the original classification.

ASTER Global Digital Elevation Model (ASTER GDEM) data were used to derive terrain data. ASTER GDEM data were accessed from http://gdem.ersdac.jspacesystems.or.jp using a map of the study area. The data are available at a resolution of 30 m per pixel. Topographic ruggedness was calculated using the VRM (vector ruggedness measure) (Sappington et al. 2007) using an ArcGIS script in a 3×3 window size (http://arcscripts.esri.com/ details.asp?dbid=15423). It is based on a geomorphological method for measuring vector dispersion that is less correlated with slope (Sappington et al. 2007). The dimensionless ruggedness number ranges from 0 (flat) to 1 (most rugged).

Using the land cover map of the study area (Department of Survey), a map of distance to the village was prepared by classifying forest area into five categories based on its proximity to the nearest village (less than 250, 500, 750, and 1,000 m and greater than 1,000 m) in ArcGIS. This map was rasterized at a resolution of 30 m.

Preparation and evaluation of the suitability map

We used approximately 76% of data (collected along 325.8 km of transects in 2008 and 2009) for evaluating species-habitat associations (model development) and remaining dataset for model verification. To see species-habitat associations, we defined the availability (p) for each category of environmental variable as the proportion of all records in all clusters, for which the corresponding value of the environmental variable was 'true' (e.g. in which the slope was between 15° and 30° if p for the environmental variable 'slope between 15° and 30°).

For each species and environmental variable, we defined species usage (r) as the proportion of records for which the corresponding value of this environmental variable was 'true' and associated with signs of this species occurrence (e.g. r value for barking deer in areas

Model	Barking deer			Himalayan goral			Himalayan serow					
	Parameter estimates	SE	Wald	P value	Parameter estimates	SE	Wald	P value	Parameter estimates	SE	Wald	P value
Topographic variables												
Slope	-0.052	1.010	47.886	0.000	0.066	0.01	99.32	0.000	0.020	0.010	3.810	0.050
Ruggedness	-3.363	0.940	12.810	0.000	0.908	0.76	1.446	0.229	5.130	1.960	6.83	0.009
Constant	2.495	0.320	62.020	0.000	-2.492	0.25	98.34	0	-1.8	0.340	31.400	0.000
Nagelkerke R^2		0.335				0.411				0.331		
AUC		0.805				0.830				0.800		
Distance to the village	0.002	0.000	45.706	0.000	0.001	0.000	66.345	0.000	0.001	0.000	33.365	0.000
Constant	-1.299	0.209	38.553	0.000	-1.513	0.201	56.458	0.000	-1.514	0.292	26.967	0.000
Nagelkerke R ²		0.241				0.217				0.261		
AUC		0.786				0.741				0.837		

Table 2 Results of binomial logistic regressions of the selected habitat variables

with a slope between 15° and 30° was calculated as the ratio of the number of records of signs of the presence of barking deer divided by the total number of sampling points where the slope was between 15° and 30°).

We then calculated Jacob's index (*D*) as $D = \frac{r-p}{r+p-2rp}$ (Jacobs 1974) for each species and each category of environmental variable. The value of *D* varies from 1 for maximum association to -1 for no association.

For each species and each of the four main environmental variables (slope, topographic ruggedness, forest type and distance to the village), a suitability map was constructed in ArcGIS as follows. Each pixel of the study area was categorized into one of the five classes of habitat suitability according to the D value corresponding to this pixel and of environmental variables and species in question (described in Figure 2 and Table 3). The final Dvalue of all different categories of environmental variables is given in Table 4.

For each species, the four suitability maps (one for each of the four environmental variables) were multiplied using the map calculator in ArcGIS 9.2 to create a single suitability map for the species (Liu et al. 2001; Dayton and Fitzgerald 2006). This is a better method than a weighted summation because it eliminates optimistic prediction (e.g. 0 suitability in any of the environmental variables gets unsuitable score finally). Furthermore, environmental variable here are already weighted while assigning suitability scores based on Jacob index (D). The map suitability value calculated in this way ranged from 0 (no suitability) to 144 (very high suitability). Finally, we derived four categories (poorly suitable, moderately suitable, suitable and highly suitable) from this continuous scale of 0 to 144 based on the multiplication of three suitability values for each category (e.g. 4 is the value for a highly suitable category of environmental variable. The multiplicative value of the three highly suitable categories is 64. Thus, a pixel with a value greater than 64 was classified as highly suitable in the final map). Thus, we classified each pixel as follows: 0 - unsuitable, 1 to 8 - poorly suitable, 9 to 27 - moderately suitable, 28 to 64 - suitable and greater than 64 - highly suitable. Because we ranked some environmental factors as 0 and used a multiplicative approach, the final map had many areas with a value 0, indicating that they are unsuitable for the species in question regardless of the suitability of the other environmental variables.

In surveys of large mobile wildlife, absence data are in fact 'pseudo absence', because it is not possible to be certain that the particular location is not used by the target species. We, therefore, used a presence-only data for model evaluation that discriminates a model predicting presence everywhere from a more contrasted model by using predicted-to-expected (R) ratio of each habitat suitability category (Boyce et al. 2002) as $R = P_i/E_i$, where P_i is the proportion of presence records for evaluation points with a habitat suitability class *i* and E_i is the relative area covered by the suitability class *i*. The basic assumption of this evaluation procedure is that a good suitability map should be based on a better evaluation of presence than expected by chance, resulting in R > 1. Thus, highly suitable habitats should have a proportionally higher number of presence records (Hirzel et al. 2006). We calculated the Boyce index $(B_{\rm b})$ by computing a Spearman rank correlation between R and class rank, which varies between -1 and 1. Positive values indicate a model, whose predictions are consistent with the distribution of presences in the dataset evaluated, negative values indicate an incorrect model and values close to zero indicate that the model's prediction is not different from random (Boyce et al. 2002; Hirzel et al. 2006). The model evaluation was carried out using an independent dataset of species presences that was collected along 104 km of transects. It included 52 records of the



presence of barking deer, 63 of Himalayan goral and 38 of Himalayan serow.

We also evaluated whether the observed frequencies of occurrence of the three species in each category of habitat quality were different from those expected based on the availability of habitat categories using a

Table 3 The conversion of Jacob's index (D) into corresponding suitability values

Jacob's index (D) range	Suitability categories	Suitability value
-1	Unsuitable	0
−1 to −0.5	Poorly suitable	1
-0.5 to 0	Moderately suitable	2
0 to 0.5	Suitable	3
0.5 to 1	Highly suitable	4

The lower bound of the class is not included in the corresponding class.

chi-square goodness of fit test. Bonferroni confidence interval (adjusted):

$$p_i - z_{(1-\alpha/2k)} \sqrt{p_i(1-p_i)/n} \le p_i \le p_i + z_{(1-\alpha/2k)} \sqrt{p_i(1-p_i/n)}$$

was used to determine, which habitat categories were drivers of significant changes in the model's prediction. Here, p_i is the proportion of presence signs in the *i*th suitability category, *n* the sample size (number of recorded presences) and *k* the number of parameters used in the model.

Results

Logistic regression revealed the discriminatory power of the habitat variables for indicating the presence of all the species (Table 2). *Barking deer* was not recorded in areas with a highly rugged and steep terrain and those close to

Variable	Barking deer	Himalayan goral	Himalayan serow
Slope (degrees)	Suitable (<30), moderately suitable (30 to 60), poorly suitable (60 to 75), unsuitable (>75)	Highly suitable (45 to 75), suitable (75 to 90), moderately suitable (30 to 45), poorly suitable (<30)	Suitable (30 to 75), moderately suitable (15 to 30), poorly suitable (0 to 15, 75 to 90)
Ruggedness	Suitable (<0.05), moderately suitable (0.05 to 0.44), poorly suitable (0.44 to 0.99)	Suitable (>0.05), poorly suitable (<0.05)	Suitable (0.05 to 0.19), moderately suitable (>0.19), poorly suitable (>0.05)
Distance to the nearest village (metres)	Suitable (>500), moderately suitable (250 to 500), poorly suitable (>250)	Suitable (>750), moderately suitable (250 to 500), poorly suitable (<250)	Highly suitable (>1,000), suitable (750 to 1,000), moderately suitable (500 to 750), poorly suitable (250 to 500), unsuitable (<250)
Forest type	Highly suitable (STSF), suitable (LTBLF, TMF, TBLF), moderately suitable (BA, STPBLF), poorly suitable (SABLF, RARA), unsuitable (SPF, UTCF, SAMF, SACF, AM)	Highly suitable (STSF), suitable (SPBLF, TBLF, UTCF, RARA), moderately suitable (LTBLF, TMF, SABLF, SAMF, SAMF), poorly suitable (SPF, AM, BA)	Highly suitable (STSF, UTCF), suitable (SACF, SAMF, SABLF), poorly suitable (SABLF, TMF, RARA), unsuitable (AM, BA)

Table 4 Suitability rating of the four factors described in Table 3

human settlements (Figure 2); it occurred mainly in subtropical sal forest, lower temperate broad-leaved forest, temperate mixed forest and temperate broad-leaved forest (Figure 2). Topographic variables were stronger indicators of the presence (Nagelkerke R^2 0.335, AUC 0.805) than the distance to the nearest village (Nagelkerke R^2 0.241, AUC 0.786) for this species. Himalayan goral occurred mainly in subtropical sal forest, subtropical pine broad-leaved forest, temperate broad-leaved forest and rocky and grassy areas (Figure 2). Topographic variables were stronger indicators of the presence (Nagelkerke R^2 0.411, AUC 0.830) than distance to the nearest village (Nagelkerke R^2 0.217, AUC 0.741) for this species (Table 2). Himalayan serow occurred mainly in subtropical sal forest, upper temperate coniferous forest, subalpine coniferous forest and subalpine broadleaved forest (Figure 2). Both topography (Nagelkerke R^2 0.331, AUC 0.800) and distance to the nearest village (Nagelkerke R^2 0.261, AUC 0.837) were important indicators of the presence of this species (Table 2).

The Boyce indices (B_b) for barking deer and Himalayan goral were at their maximum theoretical limit (1), confirming excellent discrimination (Table 5). The index for Himalayan serow was also high (0.6), which indicates that the model consistently indicates a distribution for goral that accords with its distribution. Predicted-toexpected (*R*) ratio was also consistently high for the high suitability class and greater than one for the highly suitable habitat for all target species. According to Boyce et al. (2002) and Hirzel et al. (2006) such patterns in suitability maps are consistently close to reality.

Suitable habitat based on all the categories for barking deer covered 57% of the study area. Of all the suitable habitats for this species, 18%, 19%, 33% and 30% are poorly suitable, moderately suitable, suitable and highly suitable habitats, respectively (Figure 3). Approximately 79% of the signs of the presence of barking deer occurred

in the suitable and highly suitable habitats. The records of barking deer in the predicted habitat categories were disproportionate relative to their availability ($\chi^2 = 11.95$, df = 3, P < 0.007) as this species was recorded in highly suitable habitats significantly more frequently than expected by chance (Table 6).

Suitable habitat in terms of all the categories for Himalayan goral covered 67% of the study area. Of all the suitable habitats, 38%, 26%, 32% and 4% were poorly suitable, moderately suitable, suitable and highly suitable habitats, respectively (Figure 4). Approximately 63% of the signs of the presence of Himalayan goral were recorded in suitable and highly suitable habitats. The records of goral in the predicted habitat categories were disproportionate relative to their availability ($\chi^2 = 56.86$, df = 3, P = 0.001) as this species was recorded in highly suitable habitats significantly more frequently than expected by chance (Table 6).

Suitable habitats in terms of all the categories covered 41% of the study area for Himalayan serow. Of all the suitable habitats, 13%, 23%, 24% and 40% were poorly suitable, moderately suitable, suitable and highly suitable habitats, respectively (Figure 5). Approximately 89% of the records of the presence of Himalayan serow were in suitable and highly suitable habitats. The records of serow in predicted habitat categories were disproportionate relative to their availability ($\chi^2 = 10.84$, df = 3, P = 0.012) as significantly fewer than expected were for poorly suitable and moderately suitable habitats and significantly more for suitable and highly suitable habitats (Table 6).

Discussion

When identifying areas for conservation it is important to know the spatial distribution of good-quality habitat for the target species. We provide landscape-scale maps of the distribution of three mountain ungulates based on

	Suitability (i)	Proportion of evaluation points (<i>P_i</i>)	Relative area covered by a particular suitability class (<i>E</i> _i)	Predicted-to- expected ratio	Boyce index (Bb)
Barking deer	Poorly suitable	0.08	0.18	0.44	1.00
	Moderately suitable	0.13	0.19	0.68	
	Suitable	0.27	0.33	0.82	
	Highly suitable	0.52	0.31	1.68	
Himalayan goral	Poorly suitable	0.11	0.38	0.29	1.00
	Moderately suitable	0.25	0.26	0.96	
	Suitable	0.44	0.32	1.38	
	Highly suitable	0.19	0.04	4.75	
Himalayan serow	Poorly suitable	0.03	0.13	0.23	0.60
	Moderately suitable	0.08	0.23	0.35	
	Suitable	0.37	0.24	1.54	
	Highly suitable	0.53	0.40	1.33	

Table 5 Boyce index (B_b) of the habitat suitability maps for barking deer, Himalayan goral and Himalayan serow

High values indicate a high consistency in the evaluation of the datasets, and a value greater than 1 indicates good suitability.

habitat suitability. The Boyce index and predicted-toexpected ratio (R) show that the maps accurately describe the general distribution of suitable habitats and distribution of the target species. These maps reveal that all three ungulates are present significantly more often in highly suitable habitats than expected based on the availability of this habitat. Thus, wildlife mainly occurs in highly suitable habitats, which are sparsely distributed in this region, mainly due to human modification of the landscape, which has greatly reduced the proportion of the habitats in region that are of high quality (Fischer and Lindenmayer 2007).

The map for barking deer shows that there is a large area of suitable habitat available for this species throughout the study area (Figure 3), which is made up of 66% of suitable and highly suitable habitats. This may be because barking deer is adapted to live in a wide variety of habitats (Ohtaishi and Gao 1990; Prater 1990; Roberts 1999; Paudel and Kindlmann 2012a) including degraded forest near human settlements (Oka 1998; Paudel and Kindlmann 2012a). However, although there is a large area of high-quality habitat for barking deer in the middle region, it needs to be urgently conserved, and poaching there reduced because human activities in non-protected areas are likely to increase in the absence of a conservation program. The suitable habitat for goral is scattered throughout the study area (Figure 4) but occurs mainly in the south (along the boundary of the Bardia National Park) and the north of the region (along mountain ridges). Highly suitable habitat makes up only 4% of the suitable habitat for Himalayan goral. This indicates that Himalayan goral occurs abundantly in small, highly fragmented and patchily distributed habitats, as previously reported by Hajra (2002), who found that less than 1% of the area is highly suitable for goral in the Sivalik hills in Uttaranchal, India. The steep grassy slopes, which are the most preferred habitat of goral (Cavallini 1992; Mishra and Johnsingh 1996; Fakhar-I-Abbas et al. 2008; Paudel and Kindlmann 2012a), are now almost exclusively used for agriculture and settlements. The map for Himalayan serow shows its habitat as patchily distributed in the south (along the boundary of the Bardia National Park) and north (along mountain ridges) of the study area (Figure 5). Suitable habitats of all categories cover only 40% of the study area, which indicates that the area of high-quality habitats (suitable and highly suitable) is very small for Himalayan serow, even though they comprise a relatively large proportion of all categories of suitable habitats (64%). Thus, the habitat suitability maps for serow indicate that it is important to increase habitat quality and maintain corridors connecting core habitats in order to ensure the long-term survival of this species.

We provide a simple way to identify high-quality habitat for ungulates in a mountain landscape. This approach primarily results in the production of a map of the spatial distribution of the preferred habitats of the target species. It has several advantages over other methods. Many investigators select habitat variables based on the literature and expert judgment. In our study, we first tested whether habitat variables can be used to predict the presence and absence of species using logistic regression and derived suitability indices for particular habitat variables based on Jacob's index (D). Furthermore, the multiplication approach used to combine habitat variables with suitability results in values of 0 (not suitable) and 1 (poorly suitable) and reduces the incidence of overoptimistic predictions (Dayton and Fitzgerald 2006; Gavashelishvili and Lukarevskiy 2008). Another possible criticism may be that too few variables are included in the model.



	Predicted suitability category (<i>i</i>)	Proportion of suitable category (p _i)	Observed frequency in the <i>i</i> th habitat category (O)	Expected frequency of species observation in the <i>i</i> th habitat category (<i>p</i> _i O+)	Proportional frequency in the habitat category (p _i O/p _i O+)
Barking deer	Poorly suitable	0.18	4	9.36	0.08
	Moderately suitable	0.19	7	9.75	0.13
	Suitable	0.33	14	16.91	0.27
	Highly suitable ^a	0.31	27	15.98	0.52
Himalayan goral	Poorly suitable	0.38	7	24.11	0.11
	Moderately suitable	0.26	16	16.43	0.25
	Suitable	0.32	28	20.19	0.44
	Highly suitable ^a	0.04	12	2.27	0.19
Himalayan serow	Poorly suitable ^a	0.13	1	4.89	0.03
	Moderately suitable ^a	0.23	3	8.70	0.08
	Suitable ^a	0.24	14	9.18	0.37
	Highly suitable ^a	0.40	20	15.24	0.53

Table 6 Observed and expected occurrence of three species in each of the four habitat categories

O+, total number of records in all habitat categories for each species. ^aSignificant at P < 0.05 after Bonferroni correction.

Studies on habitat suitability and distribution of wildlife show that accurate predictions can be made on the basis of a few variables (Liu et al. 2001; Dayton and Fitzgerald 2006; Gavashelishvili and Lukarevskiy 2008).

Biased sampling can result in an erroneous resource selection function. For example, transects that predominately follow a common habitat and topographic feature might not include all the important habitat features for a particular target species. The areas surveyed included significantly representative proportions of the different slopes ($r^2 = 0.97$) and topographic ruggedness ($r^2 = 0.97$), but not distances to the nearest village $(r^2 = 0.78)$ and forest type ($r^2 = 0.69$). These sampling biases are a result of little sampling within 250 m of the periphery of villages (beyond 250 m from villages, $r^2 = 0.98$), which are mostly covered by highly degraded forest such as bushy areas and subtropical pine forest (for subtropical pine forest without bushy areas $r^2 = 0.91$). These are poor habitats for all species. We argue that biases introduced by not sampling these habitats do not affect the allocation of the suitability index because it is very unlikely that the target species occur in these habitats.

Generally, the prediction of those sites that are occupied is more successful than of those that are not (Osborne et al. 2001). Thus, the maps need to be evaluated in an ecological context (Fielding and Bell 1997). For example, serow locally extirpated from mid-regions although there are large fragments of suitable habitat (Paudel and Kindlmann 2012b). Hence, further research is necessary to determine whether the absence of serow in many suitable habitats is either an effect of small patch size, isolation or human influence or a combination of these factors. We argue that some external factors, such as hunting, might result in the local extinction of certain species. We found that serow in small areas of suitable habitat are more likely to be hunted than those in large areas because small areas are more often monitored by hunting groups (unpublished data). We could not use hunting data in developing the model as such data are difficult to obtain and its spatial precision is uncertain because of the mobile nature of hunting.

Habitat loss and wildlife hunting pose a formidable challenge for wildlife conservation in Nepal's mountains (Jackson 1979; Paudel 2012). Long-term survival of wildlife depends on sufficiently large areas of suitable habitat and opportunities for dispersal between such areas (Harrison 1991; Hanski 1999). Thus, we propose that areas supporting suitable habitats for all three mountain ungulates be designated as conservation areas, especially in areas adjoining the northern boundary of Bardia National Park, along the mountain tops in the middle part and forested areas in the northern part. Except in the national parks (Bardia National Park in the south and Shey Phoksundo National Park in the north), the quantity and quality of habitat is likely to decrease due to human activities such as collecting wood for fuel, harvesting timber and clearing forest for agriculture. Once forests that are easy to access or close to human settlements are exhausted, those in more remote areas at higher altitudes will be exploited. It is therefore important to conserve large patches of habitat and restore connectivity between core areas to ensure species survival. This will enable not only survival of the three target species but also others native to the midhills. The mountain ranges, where suitable habitat for serow and goral exists, in the mid and northern parts of the study area, also provide occasional habitats for a small population of blue sheep (Pseudois nayaur), Himalayan musk deer (Moschus chrysogaster)





and Himalayan black bear (*Ursus thibetanus*) (unpublished data). These species are important prey of snow and common leopards (Prater 1990; Roberts 1999). We argue that conservation of core habitats and their connectivity leads to conservation of isolated wildlife populations and their predators such as snow and common leopards because carnivores tend to occur where their preferred prey are abundant (Carbone and Gittleman 2002).

Conclusions

The habitat suitability maps provide important baseline information for landscape-level conservation over a large altitudinal range in the western midhills of Nepal. The maps show that the majority of the suitable habitats are clustered mostly either in the northern or southern regions of the study area, whereas the mid region harbours small but highly fragmented suitable habitats. The size and spatial configuration of the suitable habitats is critical for the long-term survival of wildlife (Andrén 1994; Hanski 1999; Mech and Hallett 2001). We suggest further studies on connectivity and patch occupancy of wildlife. This is true especially for Himalayan serow that is patchily distributed in isolated habitats. The absence of serow in many large areas of suitable habitat shows the need for the restoration of corridors between such habitats (Paudel and Kindlmann 2012b). Furthermore, the map identifies probable sites for potential reintroduction of serow in areas within its historical range in the midhills of Nepal. Like serow, Himalayan goral is patchily distributed, with high-quality habitats confined to the Churia hills in the southern part of the area, which is a relatively inaccessible area with a rich cover of grass. Therefore, conservation of existing high-quality habitats should be the main focus of the conservation of Himalayan goral.

Here, we use a multi-species approach to identify the problems of conserving wildlife in Nepal. Although the use of surrogate information for certain species is questioned (Bonn and Gaston 2005), but recommended in the absence of other assessment options (Landres et al. 1988), we chose three particular species because they occupy a range of habitats that include those of many other species of wildlife. An extensive survey of the occurrence of carnivores such as leopards (*Panthera pardus, Uncia uncia*) and Himalayan musk deer in the study area is not possible because they are rare and the topography of the region is highly rugged. Hence, the habitat suitability maps of the species studied can be an effective tool for evaluating their conservation needs and designating areas for conservation.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

PKP conceived and executed the study, collected the field data and performed the modelling analyses. MH carried out the vegetation categorization of the study area using remote sensing. PK helped to draft the manuscript. All authors read and approved the final manuscript.

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