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Breeding habitat and nest-site selection of Bearded Vulture *Gypaetus barbatus* in the Annapurna Himalaya Range of Nepal

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Quantitative studies on nesting habitat selection are important to understand and predict the resource requirements for breeding habitat. In this study, we analysed nest-site (cliff) and territory selection patterns of the Bearded Vulture in the Annapurna Range of the Himalayas (Nepal). Our study area represents high-elevation mountain range systems, where information on nest selection is lacking, despite having the largest remaining populations of Bearded Vultures in the world. Our models indicated selection patterns at both nest and territory spatial scales that are consistent with previous studies at lower altitudes (Pyrenees, the Caucasus), such as a preference for landscape patches with greater food availability. However, our models also indicated selection patterns that are probably a response to the higher altitudes and sheer reliefs of the Annapurna massif, such as avoidance of the steepest slopes and selection of cliffs facing south and west for nest-sites. We did not detect an impact of human activities on the distribution of nests or territories. However, the Annapurna massif is experiencing development of infrastructures (e.g. road construction). Further research efforts will be needed to monitor human impacts on Bearded Vulture populations in the Annapurna Range, as this is a global stronghold for this species.

Keywords: breeding habitat, cliff, foraging area, high altitudes, territory.

The quality of a nest-site and territory is one of the main determinants of reproductive success and survival in territorial birds (Cody 1985). As such, there should be relatively strong habitat selection patterns for nest-sites and territories in birds. Given the cost of searching for a new nest-site and territory, it has been suggested that selection will be stronger in long-living territorial organisms that may use the nest and territory for many consecutive years (Krüger 2002, Krüger *et al.* 2015). In addition to identifying key determinants of individual fitness, quantitative nest-site and territory selection studies are instrumental in the conservation of endangered territorial species, as they inform habitat management policies (González *et al.* 1992, Sánchez Zapata & Calvo 1999, Suárez *et al.* 2000) and assist in other conservation measures such as reintroductions (Donázar *et al.* 1993).

The Bearded Vulture *Gypaetus barbatus* is the most mountain-specialized Old World vulture in the world. In recent years, the distribution and

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breeding density of the species has been largely reduced in most of its range (Xirouchakis *et al.* 2001, Margalida *et al.* 2008b, Acharya *et al.* 2010, Krüger *et al.* 2014a, Ogada *et al.* 2016). Based on small and declining populations, the Bearded Vulture is listed as a Vulnerable species in the national Red Data book of Nepal (Inskipp *et al.* 2016). Although factors for population declines vary among different geographical areas, the overall declines of this species are primarily attributed to human persecution, unintentional poisoning, electrocution, and collision with powerlines and wind turbines (Margalida *et al.* 2008b, Reid *et al.* 2015).

Selection of nesting cliffs and foraging areas by Bearded and other vulture species depend on a combination of climatic, geographical and other environmental factors including food availability and human disturbance within the territory (Donázar *et al.* 1993, Gavashelishvili & McGrady 2006, Margalida *et al.* 2007, 2008a, Reid *et al.* 2015). Bearded Vultures select territories in rugged terrain with low human disturbance and avoid the highest altitude areas where food resources may be scarce. However, these studies have been carried out in mid-elevation mountain ranges (Pyrenees, the Caucasus, Drakensberg). No information is available for the Asian mountain ranges (e.g. Himalaya, Karakorum, Hindu-Kush) that cover greater altitudinal and environmental ranges. High-altitude ranges in Asia are home to some of the largest populations of this vulture species (BirdLife International 2017), yet factors affecting selection of nesting and foraging sites in these birds is not known. From a conservation perspective, studies on habitat selection in Bearded Vulture would assist in the identification of those landscapes or components of the landscape most relevant for the species. Nest-site selection studies have proven valuable in Europe, particularly in the Alps and Pyrenees, where Bearded Vultures have been reintroduced in the last few decades (Donázar *et al.* 1993, Margalida *et al.* 2015). Bearded Vulture reintroduction projects are costly (Margalida *et al.* 2017) and it is important to evaluate habitat suitability before releasing the birds in the wild (Hirzel *et al.* 2004).

Our work, quantifying nest-habitat selection of the Bearded Vulture in the Annapurna Range of the Himalayas in Nepal, fills an important gap in our knowledge of the ecology of this territorial raptor and particularly informs the ecology of a stronghold population, given the global decline of the species. Specifically, we have analysed the nest-site selection of Bearded Vulture in relation to geographical, environmental and human disturbance factors in the Annapurna Range at two spatial scales: cliff and landscape. The former scale describes microhabitat characteristics preferred by Bearded Vultures for nesting and the latter gives insights into the characteristics of the landscape that are selected for breeding territory, providing information on habitat selection not only for nesting but also for other key activities such as foraging.

METHODS

Study area and data collection

This study was conducted in the Annapurna Himalaya Range (28°57′43.99″N, 83°48′10.4″E), in the central Himalaya of Nepal. Between 2012 and 2016, we surveyed suitable nesting cliffs from several trails and observation points in the Mustang, Myagdi and Kaski districts (Fig. 1) to the north and northwest of the Annapurna Himalaya Range, an area of over 1000 km^2. Sampling was conducted during the incubation and chick-rearing period between November and May. Using information also from local people and nomadic herders we identified 17 active nests of Bearded Vultures. An additional five active nests were opportunistically recorded in Syangja, Arghakhanchi, Kalikot and Jajarkot districts to the south and west of the Annapurna Himalayan Range, totalling 22 Bearded Vulture nests for analysis (Fig. 1). Twenty-two cliffs without nests were randomly selected (Donázar *et al.* 1993) as controls. Random points were obtained using a random point generator in ArcGIS 10.3 (ESRI, Redlands, CA, USA). As random points were not exactly located over cliffs, the unoccupied cliff nearest to each random point was chosen using Google Earth.

Nest characterization was assessed at two spatial scales: cliff and breeding territory, using ArcGIS and Googel Earth. To estimate cliff variables (Table 1), we used a 1-km buffer around the nesting cliffs or nest locations and random cliffs. Similarly, we used a 15-km buffer radius around the nest locations and random cliffs to collect the breeding territory scale variables (Table 2). The buffer of a 15-km radius used was based on foraging area of GPS-tracked

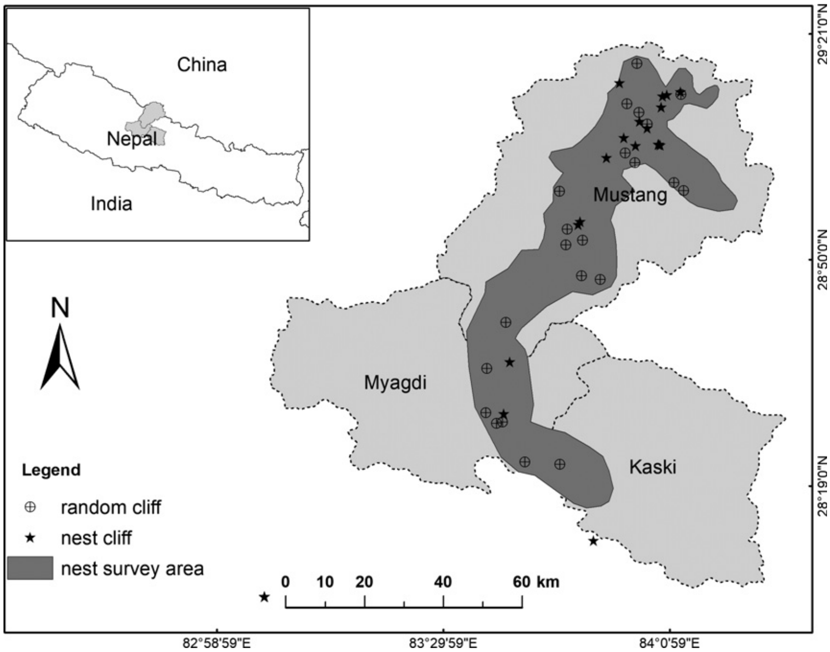

Figure 1. Location of nest survey area, nesting and random cliffs.

territorial adult Bearded Vultures (700 km^2) in Nepal (Subedi *et al.* 2017) and similar studies in South Africa (Krüger *et al.* 2014b) and Europe (Margalida *et al.* 2016). Topographical variables were collected using a Geographical Information System (GIS). We used the globeland30-global land cover dataset with 30-m resolution (Chen *et al.* 2015), and 'hole-filled' Shuttle Radar Topographic Mission (SRTM) Digital Elevation Model (DEM) layer, STRM3 (03 arc s, or ~90 m resolution; Jarvis *et al.* 2008). Human population data were compiled from the 2011 census report of Nepal (Government of Nepal 2012). Pairwise correlation analyses did not detect strongly correlated variables ($r < 0.7$) (Dormann *et al.* 2013).

Statistical analysis

Nest-site selection was examined by testing for differences between the characteristics of nesting cliffs ($n = 22$) and random cliffs ($n = 22$) at the cliff (Table 1) and territory (Table 2) scales. First, we assessed the differences for each scale and for each environmental variable using a univariate generalized linear model (GLM) (McCullagh & Nelder 1989), assuming a binomial distribution of error and a logistic link function. The response variable was either one (actual nesting cliff) or zero (random cliff) (Donázar *et al.* 1993, Margalida *et al.* 2008a). Because the responses to single variables can be affected by correlation among explanatory variables (thus identifying spurious responses), we also developed a multivariate model for each scale. Variable selection in the multivariate model followed a stepwise approach, using the Akaike information criterion (AIC) for model selection. No variables were included in the model if they did not decrease AIC by more than two units. All the statistical analysis were performed in RStudio 1.0.136 (RStudio Team 2016) using R 3.4.1 (R Core Team 2017).

RESULTS

Sampled nest cliffs were distributed between 1445 and 4600 m a.s.l. (3141 ± 1003.0 sd), most of them facing south (Table S1). Univariate GLMs (Table 3) showed significant responses for cliff selection with the following variables: cliff aspect, distance to water/river, distance to village, length of road, percentage of agricultural land cover and percentage of area facing SW within a 1-km radius of the nest. The variables with the greatest explanatory power were distance to water (D^2 = 30.5%), with a negative response, and cliff

Table 1. Variables used and methods of measurement to analyse habitat selection of the Bearded Vulture at the cliff scale.

Variable	Description	Method
Topography		
Cliff elevation	Altitude of the nest/cliff above sea level (m)	GIS
Cliff aspect	Orientation of the cliff face at the level of nest. Orientation of the cliffs was scored following the approach of Donázar *et al.* (1993) and Margalida *et al.* (2008a) based on dry wind and solar radiation from S to W, in the afternoon hours: 1 = SW or S or W, 2 = NW or SE, and 3 = NE or N or E	GIS
% *Aspect*	% of each aspect category (N, NE, E, SE, S, SW, W and NW) within 1-km radius	GIS
Slope	Steepness of the cliffs (in degrees)	GIS
Mean slope	Mean steepness of the area (in degrees) within 1-km radius of cliffs	GIS
Land uses		
Distance to water	Linear distance to nearest river or water sources (m)	Google Earth
% *Land cover*	Land use cover in % (forest, shrub, grassland, barren, agriculture, snow) within 1-km radius of cliffs	GIS
Human disturbance		
Distance to village	Linear distance to nearest settlement/village (m) from the cliffs	Google Earth
Population	Human population in the nearest village	Government report (census 2011)
Distance to road	Linear distance between the nests/cliffs to the closest motor road (m)	Google Earth
Km road	km of paved and unpaved (seasonal and regular) road within 1-km radius of nests/cliffs	Google Earth

Note that '% Aspect' represents eight different continuous variables.

Table 2. Variables and methods of measurement used to analyse habitat selection of the Bearded Vulture at the territory scale.

Variable	Description	Method
Topography		
Elevation	Mean elevation within 15-km radius of cliffs (m)	GIS
% *Aspect*	% of each aspect category (N, NE, E, SE, S, SW, W and NW) within 15-km radius of the cliffs	GIS
Mean slope	Mean steepness of the area (in degrees) within 15-km radius of cliffs	GIS
Land uses		
% *Land cover*	Land use cover in % (forest, shrub, grassland, barren, agriculture, snow, development) within 15-km radius of cliffs	GIS
Human disturbance		
Population	Human population within 15-km radius of cliffs	Government report (census 2011)
Km road	km of paved or regular motor road within 15-km radius of cliffs	Google Earth

Note that '% Aspect' represents eight different continuous variables.

aspect (D^2 = 25.6%), with a negative response to aspects N-NE-E and NW-SE. The highest number of nests (n = 14, 64%) were in cliffs facing either southwest, south or west. Regarding the orientation of the area around the nest (% Aspect variable), the percentage of area facing SW within a 1-km radius of the nest had a high explanatory power with a positive response (D^2 = 18%), indicating a similar relationship with cliff aspect. At this scale, our models also indicated a positive response to the percentage of agricultural land (D^2 = 10%), the length of roads (D^2 = 15.4%) and a negative response to the distance to villages (D^2 = 9.2%) (Table 3). At the scale of breeding territory, our models showed a negative response to both the percentage snow cover (D^2 = 17.5%) and the mean slope (D^2 = 8.3%).

The best-fit model for nesting cliff selection by Bearded Vulture was obtained using the variables distance to water resource, cliff aspect, percentage of agricultural land and mean slope (Table 4). Inclusion of these variables produced a good model fit (D^2 = 67.8%). The best model for breeding territory was less explanatory (D^2 = 24%) and included two variables: percentage of snow cover and mean slope.

Table 3. Univariate GLMs to compare the variables characterized nesting and random cliffs and their territories.

	Cliff			Breeding territory		
Variables	Estimate	*Pr*(> |*z*|)	D^2	Estimate	*Pr*(> |*z*|)	D^2
Topography						
Cliff aspect (NW, SE)[a]	−1.897	0.018*	0.256			
Cliff aspect (NE, N, E)[a]	−3.738	0.002**	0.256			
% Aspect (SW)	0.068	0.016*	0.183	–	–	–
Mean slope	–	–	–	−0.159	0.035*	0.083
Land uses						
Distance to water	−0.002	0.004**	0.305			
% Agriculture cover	0.083	0.04*	0.100	–	–	–
% Snow cover	–	–	–	−0.223	0.016*	0.175
Human disturbance						
Distance to village	−0.001	0.033*	0.092			
Length of road	0.001	0.007**	0.154	–	–	–

The variables are significant at: *P = 0.05, ** P = 0.01. D^2 = explained deviance. [a]Cliff aspect is a single categorical variable with a unique D^2 value; slope estimates of the two categories with significant responses are shown.

Table 4. GLMs for nesting cliff selection and breeding territory using binomial distribution error and a logistic link function.

Models/variables	Estimate	*Pr*(> |*z*|)	AIC	D^2
Cliff scale				
Distance to water/river	−0.004	0.048*	46.39	0.305
Cliff aspect (NW, SE)[a]	−6.362	0.051	35.50	0.549
Cliff aspect (NE, N, E)[a]	−9.876	0.038*	35.50	0.549
% Agriculture cover	0.209	0.076	32.96	0.592
Mean slope	−0.287	0.093	31.63	0.678
Breeding territory scale				
% Snow	−0.213	0.015*	54.34	0.175
Mean slope	−0.166	0.06	52.35	0.240

Each variable is listed in order of inclusion in the model. D^2 = explained deviance. [a]Cliff aspect is a single categorical variable with a unique D^2 and AIC value; slope estimates for the two categories with significant responses are shown. The variables are significant at: *P = 0.05.

DISCUSSION

Assessment of the habitat selection patterns for nest location and breeding areas is key to understanding the ecology of territorial birds (Cody 1985). Our study provides the first quantification of nest-site (cliff) and territory selection patterns of the Bearded Vulture in high-elevation mountain range systems, where the largest populations of the species remain. Our studied population was at a higher altitude (mean nest altitude = 3141 m a.s.l., Table S1) than other previously studied populations in the Pyrenees (1333 m a.s.l., Donázar *et al.* 1993) and the Caucasus (1883 m a.s.l., Gavashelishvili & McGrady 2006). As more broadly discussed below, our models indicate selection patterns at both spatial scales that are consistent with previous studies, such as a preference for those landscape patches with, probably, more availability of food. However, our analyses also indicate selection patterns that can be understood as a response to the higher altitudes and greater reliefs of the Annapurna massif, such as avoidance of the largest slopes and selection of cliffs facing south for a nest location. From an applied perspective, our results constitute a first step in identifying those landscape components that may be relevant for the management of this species in high-altitude mountains, such as the Annapurna Himalaya Range.

Nesting cliff

The explained deviance of the models at the cliff scale (D^2 = 67.8%) was higher than in similar work in Europe and the Caucasus (Donázar *et al.* 1993, Gavashelishvili & McGrady 2006), indicating that our model probably captured the main environmental variables correlated with nesting cliff selection in the Annapurna region of Nepal. Distance to water from the nesting cliff had the highest explanatory power in the cliff selection model. This variable is first in the multivariate model (Table 4), with the remaining variables also contributing large amounts of the explained variance, suggesting that this relationship is not simply due to a spurious relationship with other variables. Rather than a direct relationship, we hypothesize that this negative relationship could be due to a higher availability of food near rivers. In particular, in our study area, livestock carcasses when not buried are usually disposed of in rivers (T. R. Subedi unpubl. data) and could redistribute carcasses along their length. Similarly, animal bones from slaughterhouses in the Mustang area are generally thrown into rivers (T.R. Subedi pers. obs.). Bones and corpses unconsumed by vultures during sky burials (a funeral practice to feed human corpses to vultures) are also placed in rivers. This response, together with the selection for agricultural land that enters third in the model (Table 4), is in agreement with previous studies that show selection for landscapes with high food availability due to the presence of domestic animals (Donázar *et al.* 1993, Gavashelishvili & McGrady 2006).

In contrast to previous work that showed no preference for particular aspects for nest location (Donázar *et al.* 1993, Gavashelishvili & McGrady 2006), cliff aspect was the second variable to enter into our nesting cliff model. Adding this variable along with distance to water increased the combined explained deviance by > 24% (D^2 = 54.9%). This increase is similar to the explained deviance of the univariate model, indicating that the effects of the two variables are independent (not due to the correlation between explanatory variables). Our study showed selection for cliffs with a south to west aspect. We suggest two non-exclusive alternative explanations for this pattern. First, this orientation avoids a cold north-facing aspect, which may positively influence breeding success. Previously, the lack of a relationship with aspect (Donázar *et al.* 1993, Gavashelishvili & McGrady 2006) could be due to the lower elevation of those study areas with a less adverse climate. Secondly, by selecting cliffs with a southern aspect, the Bearded Vulture takes advantage of afternoon thermals, potentially increasing flight efficiency (Pennycuick 1972, Harel *et al.* 2016). Mean slope was not a significant explanatory variable on its own; however, when included in the multivariate model, it added 8.6% to the explained deviance. The negative relationship indicated that the 1-km area surrounding the nest was slightly less steep than randomly selected slopes. The slope at the nesting cliff and surrounding area is important to generate orographic lift used by soaring raptors for efficient flight (Pennycuick 1972, Harel *et al.* 2016). In addition, three variables (percentage of area facing SW within 1-km radius of the nest, length of roads and distance to village; Table 3) produced significant single-variable responses. However, these variables were absent in the multivariate model, indicating that these variables explain portions of the variability of the data already accounted for by the variables included in the multivariate models.

Breeding territory

At the scale of the breeding territory (15-km radius), two variables that entered into the multivariate model, snow cover and mean slope, had the same explanatory power as in the single-variable models, indicating that the effect of these variables was not related. Our model indicated that Bearded Vultures avoided locating their territory in areas with a large proportion of snow cover, as found for this species in the Pyrenees and the Caucasus (Donázar *et al.* 1993, Gavashelishvili & McGrady 2006). Flight data obtained from GPS-tracked individuals in the Alps also support this result (Bogliani *et al.* 2011). As with distance to rivers at the cliff scale, this could also be related to the acquisition of food. Bones of medium-sized domestic and wild ungulates are the preferred food items of Bearded Vulture (Brown & Plug 1990, Margalida *et al.* 2009). It has been suggested that areas without snow provide finely structured rocks which are used for bone-breaking and temporary food storage (ossuaries), especially during the chick-rearing period (Margalida & Bertran 2001, Margalida 2008). Obviously, areas covered by snow year-round do not provide food resources (livestock or wild ungulates).

Our model also indicated that Bearded Vultures select their territories with surrounding landscapes that are less steep than random choice. This response, also found at the cliff scale, is the opposite of that found in both the Pyrenees (Donázar *et al.* 1993) and the Caucasus (Gavashelishvili & McGrady 2006), where the most rugged terrain is selected. As detailed above, selection for rugged terrain has been explained in terms of the existence of thermals and availability of bone-breaking areas (Margalida & Bertran 2001). In our study, the negative relationship with mean slope may be due to the sheer reliefs of the Annapurna massif, where walls are abundant at high altitudes (up to

7000 m a.s.l.). These areas are probably impractical for bone-breaking or as ossuaries due to their close to vertical slopes, and are thus avoided by Bearded Vultures.

Our results explained less variance at the territory scale than at the cliff scale (D^2 = 24.0 vs. 67.8%). This suggests that habitat selection processes in the Bearded Vulture along the Annapurna Himalaya Range could be much stronger for nest-sites than for territories. In addition to real differences in the strength of habitat selection between spatial scales, there are two other possible reasons that could contribute to this result. First, we may be missing relevant variables at the territory scale in our models. In particular, food availability is considered an important factor for breeding habitat selection by Bearded Vulture (Donázar *et al.* 1993, Gavashelishvili & McGrady 2006). Data on fine-scale livestock and wild ungulate abundance are not available for our study area but, as in Donázar *et al.* (1993), we identified a landscape metric (in our case, distance to rivers) that probably captured spatial variations in food availability at the cliff scale. Arguably, an equivalent variable at the territory scale could be highly explanatory. Secondly, it is also possible that whereas nesting cliffs were different from each other, breeding territories (15-km radius of the nest) were more similar in terms of habitat quality. This similarity is possible given the partial overlap of the 15-km-radius territories in our study area.

Conservation implications

We did not detect any negative effect of human disturbance on nest distribution of the Bearded Vulture at either scale. Our study area is a relatively remote area of the Himalayan Mountains that is only sparsely populated and where human activities (such as resulting from roads, dense settlements) may not presently reach the threshold to have a negative impact on the distribution of nests and territories. Human impacts are not only reflected in the distribution of nests but more generally in the behaviour of the species and ultimately the productivity of the population (Donázar *et al.* 1993, Arroyo & Razin 2006, Krüger *et al.* 2015), which was not assessed in our work. Donázar *et al.* (1993) described a negative impact of paved roads on the breeding success of the Bearded Vulture. At present, only a small portion of the main road crossing the Annapurna area through the Kali Gandaki River valley is paved, but the road infrastructure is undergoing development as a main connecting route between China and India through the Tibetan plateau. As such, future research will be needed to monitor increasing human impacts on the population of Bearded Vulture in the Annapurna Himalaya Range to ensure this remains a stronghold of the species. Our work identifies landscape components in the Annapurna Himalaya Range (i.e. cliffs facing south to southwest and close to watercourses) that are relevant for the conservation of the population in this system. From a management perspective, these areas can be deemed conservation-sensitive by decision-makers in the context of environmental evaluation assessment for future developments.

This study identified habitat selection patterns that were exclusive to our study area and are likely to be a response to the higher altitudes and greater relief of the Annapurna Range. This finding highlights the challenges of applying habitat models between different study areas (e.g. Randin *et al.* 2006, Latif *et al.* 2016) and the need to develop local studies that address the characteristics of target populations. As such, management and conservation actions must be based on a sound understanding of the ecology and conservation of the species that combine knowledge of the ecology of species from elsewhere with local studies.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Mean ± sd of the variables measured at nesting and random cliffs and their respective territories.