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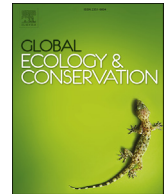
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## Short Communication

# Den-site selection at multiple scales by the red fox (*Vulpes vulpes subsp. montana*) in a patchy human-dominated landscape

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## ABSTRACT

Human-wildlife conflict impacts native wildlife populations and people in socio-economically poor areas. In the Shigar Valley, Karakoram range, Pakistan, subsistence mixed farming is the predominant land use and red foxes (*Vulpes vulpes montana*) are widely persecuted. Knowledge of the effects of human activity on fox behavior and populations in the region is lacking. We carried out 38 transect surveys within 87 sampling units of grid size 3 km × 3 km and recorded 42 resting and 24 active natal dens from 2015 to 2017. We evaluated 17 model subsets for describing probabilistic Resource Selection Functions (RSFs) predicting den occurrence at landscape, patch, and micro-habitat scales in terms of anthropogenic factors, including distance to agricultural land and roads. We also tested and controlled for associations between den occurrence and biotic and abiotic variables, including prey occurrence. We found that: 1) distance to roads negatively influenced fox den occurrence; 2) Indian pika (*Ochotona roylei*) burrow occurrence positively influenced fox den occurrence; 3) Natal dens had larger and more numerous openings than resting dens; 4) den occurrence was greatest at moderate elevations; and 5) den occurrence was negatively related to forest cover and positively correlated with shrub cover. The findings suggest that foxes do not strongly avoid human activity, and that den types are variable. Further studies are required on the function of foxes in this landscape focusing on ecosystem services such as seed dispersal, carrion removal and regulation of prey populations.

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## 1. Introduction

Global carnivore distributions overlap greatly with human dominated landscapes (Ripple et al., 2014). Such landscapes can support populations of several carnivore species, and therefore offer great conservation potential (Bender et al., 2016). However, conservation strategies often exclusively focus on protected area (PA) establishment and management, and PAs tend to be biased away from human infrastructure, such as roads and agricultural lands (Joppa and Pfaff, 2009).

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Understanding factors that allow carnivore persistence outside PAs is therefore of great importance. Carnivore conservation also differs from that of other taxa because of real or perceived impacts on human interests i.e. human-wildlife conflict (Ginsberg, 2001; Murdoch et al., 2016). The most common source of conflict between carnivores and humans is competition for resources, mainly depredation of domestic animals (Karanth and Kudalkar, 2017), which results in carnivore persecution and sometimes eradication (Karanth et al., 2014). As a result, human-carnivore conflict has resulted in significant population declines and range collapses of several species (Sillero-Zubiri and Switzer, 2004). Canids comprise one of the most prominent families of carnivores globally, with 36 taxa distributed across 13 genera from 81% of countries (Sillero-Zubiri et al., 2004; Din et al., 2013). Canids, in general, are declining across their ranges as a consequence of habitat loss, human persecution, decline in prey populations, disease and harvesting/over-exploitation (Ripple et al., 2014).

Establishment of suitable sites for denning has impacts on canid fitness, including via territory size and social organization (e.g. kit foxes (*Vulpes macrotis*), List and Macdonald, 2003; bat-eared foxes (*Otocyon megalotis*), Wright, 2006). However, the availability of such sites may be limited by habitat features, and human activity. Den location and usage is affected by the presence of other species, including predators (e.g. for swift foxes (*Vulpes velox*), Kitchen et al., 2006; red foxes (*Vulpes vulpes*), Marks and Bloomfield, 2006) and prey (e.g. for corsac fox (*Vulpes corsac*), Murdoch et al., 2009; Tibetan fox (*Vulpes ferrilata*), Wang et al., 2008; red fox, Gallant et al., 2014; Márton et al., 2016). Further, patterns may vary according to spatial scale; for example Indian foxes (*Vulpes bengalensis*) denning in a human-modified short grassland landscape, showed distinct differences between 3rd and 4th order habitat selection (Punjabi et al., 2013). Physical characteristics and function of dens also vary according to species, season and individual. In the swift fox, for example, natal dens typically have more entrances than non-natal dens (Pruss, 1999). The red fox uses dens for birthing and rearing offspring ('breeding dens') and as resting sites ('non-breeding dens') outside the breeding periods (Meia and Weber, 1992). Red foxes are central-place foragers using den sites for caching prey during both breeding and nonbreeding periods (Hewson, 1986; Arjo et al., 2003).

In Asia, 10 canid species have been described, but only six species, including red foxes, occur in Pakistan. It is assumed that most of these canid species are declining, although data are scarce (Din et al., 2013). Although red foxes (hereafter termed 'foxes') are globally widespread and very common in much of their range, they are classed as near threatened (NT) in Pakistan (Din et al., 2013). In the Karakoram and Himalayan mountain ranges of Northern Pakistan, two putative sub species occur; these are *Vulpes vulpes griffithii* and *Vulpes vulpes montana* (Tiwari, 1999; Roberts, 2005; Maheshwari et al., 2013; Zaman et al., 2020). Fox regional rarity is believed to at least in part stem from intense human persecution (Zaman et al., 2019a, 2020) in an area where retaliatory killing, for example for fox attacks on domestic hen sheds, are commonplace. Local, uncoordinated, lethal control of fox populations commonly includes filling den entrances with earth and/or smoking out foxes, and injecting poison into the corpses of fallen livestock to attract and kill scavengers (Zaman et al., 2019a, 2020). In the Karakoram range, where red foxes are sympatric with snow leopard (*Panthera uncia*) and wolf (*Canis lupus*), meso-predator release limits fox populations (Roberts, 2005; Bischof et al., 2014). Foxes are a primary predator of small mammals in the region, including Indian or Royle's pika (*Ochotona roylei*) (Schneider, 2001), and as such play a role in regulating prey populations. Habitat and resource use by foxes in the region has not previously been studied, and the effect of human activity in general is not well understood (Wang et al., 2008).

The aims of the current study were therefore to help to fill this knowledge gap by investigating the effect of human activity and prey abundance on fox (*Vulpes vulpes subsp. montana*) occurrence and behavior in terms of den site selection at the 2nd, 3rd and 4th order level. Foxes were predicted to avoid people and thus den farther away from human activity (in the form of agricultural lands and roads) than would be expected from a random distribution. Proximity to signs of prey (pika) was hypothesized to positively predict fox den occurrence, but it was expected that this association might be altered by proximity to human activity.

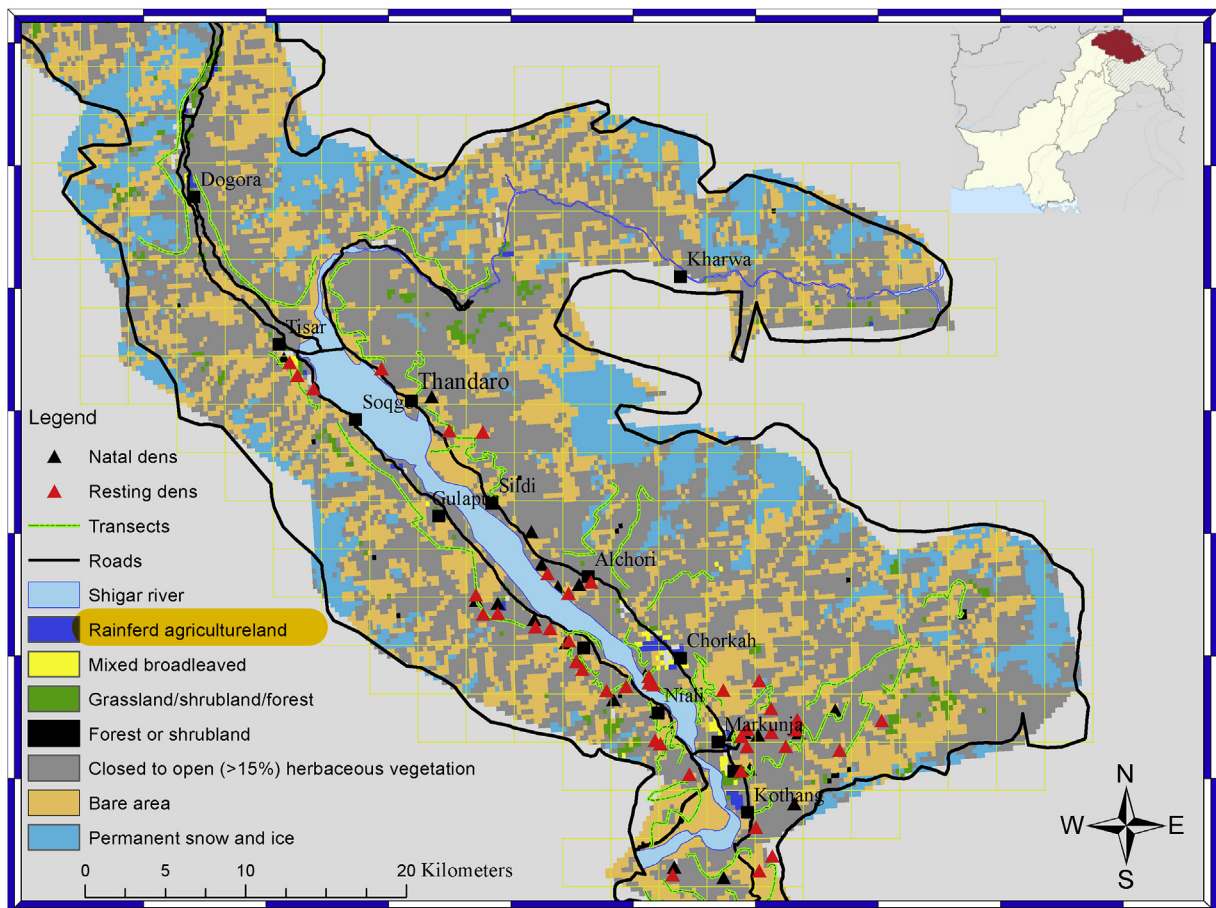
## 2. Methods

### 2.1. Study site

This study was conducted in the Shigar Valley in the Karakoram range located along the north bank of the river Indus (see Fig. 1). It lies at 25° 25'32" N latitude and 75° 42'59" E longitude and covers an area of 4373 sq. km with an altitudinal range of 2260–8611 m above sea level including K2 (8611 m), Broad Peak (8047 m), Angel Peak (6858 m) and Skil Brum (7360 m) (Zaman et al., 2020). The valleys are dry with annual precipitation of approximately 200 mm with maximum almost 600 mm at elevations of 3962 m and snow depth from 5 to 12 inches (Zaman et al., 2020). The major plant species are *Rosa webbiana*, *Hippophae rhamnoides*, and *Berberis lyceum* (Zaman et al., 2019a, b). We conducted this non-invasive study according to the regulations for animal welfare and conservation under the Gilgit- Baltistan Wildlife Preservation Act of 1975 and the Northeast Forestry University Guidelines for the Use of Animals in Research.

### 2.2. Data collection

We identified study sites that had fox dens following interviews with the occupants of 14 villages across the study area (Fig. 1) and subsequently established 38 transect lines across 87 sampling areas of grid size 3 km × 3 km. We used stratified random sampling to establish the transects based on habitat characteristics, and fox breeding den records supported by information from the interviewees. Each transect was subsequently walked twice per month by a team of 2–3 observers over



**Fig. 1.** Study sites at the landscape scale showing quantified attributes from global cover and supervised classification used for habitat types. Vegetation (shrub land/forest, 20–50%), Closed to open (>15%) herbaceous vegetation (open grassland with fox presences during three years repeated surveys in Shigar Valley, Karakoram, Pakistan).

summer (May to August) and winter (October to December) in 2015, 2016 and 2017 (excluding winter 2017) when weather conditions permitted. All den sites were recorded and equal effort (5–8 h of walking per 8–10 km) was expended in three distinct habitat types (plantation forest; bare ground, agricultural fields). The villages were approximately 3–4 km apart, which was sufficient to avoid clustering and account for variation in red fox home range sizes (Szor et al., 2008; Vanak and Gompper, 2010; Kamler et al., 2012; Munkhzul et al., 2012).

### 2.3. Den site characteristics

We characterized two types of ‘natal den’ as either an ‘earthen den’ (e.g. dug) or ‘non-earthen’ (rocks crevices, boulders) with presence of fresh cubs’ footprints and fresh domestic hen feathers. Resting dens only included earthen dens frequently used by foxes for shelter or basking. No rest sites that were not also dens were recorded within the study area (e.g., Marks and Bloomfield, 2006). We recorded the number of openings, entrance diameter and tunnel length. In multi-entrance dens, only active entrances of underground natal or resting dens were included and un-earthen were excluded. Inactive entrances were recognized by the presence of spider webs (Wang et al., 2008). We defined the tunnel length as the distance from the den entrance to the first corner in the den tunnel. Temperature (Minimum and Maximum, °C) was recorded on one day for each den site, where the den was visited once in the morning and once in the evening and the temperature taken to a depth of 1–2 m (depending on accessibility) using a Taylor 1441E Digital Waterproof Thermometer.

### 2.4. Granularity

We had no fox home range data from the study area and therefore based our survey design on spatially-referenced direct fox observations from a previous study (Zaman et al., 2019a) and data from a sympatric congeneric species – the Indian fox. Three spatial scales were considered: landscape, patch, and microhabitat, reflecting 2nd, 3rd and 4th order habitat selection



respectively, following previous authors (Johnson and Gillingham, 2008; Jiang et al., 2009, 2010; Wheatley and Johnson, 2009). All statistical analyses were performed at these three scales. We used a Euclidian distance-based approach following Conner et al. (2003), to examine the impact of dominant land use on presence of den-sites within an 800 m diameter circular area. When compared to the classification-based approach, the distance based approach has advantages in detecting the importance of edges, and flexibility in using polygons, linear data, and point features in the analysis (Home and Jhala, 2010). We used the 800 m buffer distance since it comprised an area of c., 200 ha, which is midway between annual home range sizes of male (307.9 ha) and female (164.7 ha  $\pm$  37.8SE) Indian foxes and red foxes in similar human dominated landscapes (Szor et al., 2008; Vanak and Gompper, 2010; Kamler et al., 2012; Munkhzul et al., 2012). We used a uniform distribution to generate 100 random points in each grid cell of 3 km  $\times$  3 km following Punjabi et al. (2013). After removing points from clusters within the same feature class (such as forest patches), our analyses were then conducted within the 800 m buffers around den sites, to calculate distance from den to different feature classes within the c., 200 ha area. A total of 605 such buffer zones were generated for analyses. At the den-area scale, we recorded microhabitat characteristics within 50 m of the den site, in the form of a 25 m  $\times$  25 m north oriented plot with the den-site at the centre. We measured the same variables at four putatively available points at a distance of 300 m in four cardinal directions from the den-site (Lesmeister et al., 2008). We recorded den substrate, visibility, binary presence (1) and absence (0) of active burrows of pika (Punjabi et al., 2013) and vegetation cover according to protocols described by Wang et al. (2008). We also determined the relative density, frequency, cover and importance value index (ivi) of plant species, as described by (Zaman et al., 2020). Winter was excluded from these plot-level measurements due to low vegetation height and non-detection of natal dens. We performed masked supervised and unsupervised classification use for habitat types in ArcGIS (10.2, (Jiang et al., 2010). At the landscape scale, we quantified habitat attributes for the entire study area using 2009 global forest raster layers data downloaded from <http://data.globalforestwatch.org/datasets/> and at the patch scale, we quantified detection and non-detection of den occurrence in each km2 pixel patch following Guo et al. (2017).

## 2.5. Anthropogenic factors

Human activities were considered to potentially influence resource selection at multiple scales, as measured by e.g., distance to roads and agriculture lands (Zhang et al., 1999). For each fox den, we also recorded slope, aspect, and elevation by using a spatial analyst tool in ArcMap (10.2). A 3-D digital elevation model (DEM) was created based on the 30 m contour layer of our digital map (Jiang et al., 2009). We selected UTM zone 43-N to project the map according to the projection system. We used viewshed analysis to model visibility on a triangulated irregular network (TIN) from one (e.g., a sample site) to many observation sites where the higher the viewshed value the more easily the site could be seen. We calculated the viewshed index of all survey plots using a software application within the 3D Analyst extension of ArcGIS (10.2) described by (Jiang et al., 2010) see (Table S1).

### 2.5.1. Data analysis

For each covariate and scale, initial observation (pilot) data were split into training and testing samples, and ROC was used to determine the accuracy of a classification model at the user-defined threshold value of 0.5 (Lobo et al., 2008), and area under the curve (AUC) score of  $\leq 0.7$  (Jiang et al., 2010). We investigated collinearity of explanatory variables using variance inflation factor (VIF). Variables with VIF values of  $>3$  or averaged values across all variables of  $>3$  were considered to be collinear and were thereafter removed (Cristescu et al., 2013). For den occurrences, we used logistic regression to assemble a linear combination of terrain, vegetation, and anthropogenic factors through stepwise regression methods. We selected the most parsimonious model that best explained den number and distribution. We assumed that anthropogenic threats and prey abundance were random effects on den occurrence due to random distribution. Human disturbance covariates were therefore excluded from initial analyses and later analysed separately in relation to pika burrows. We derived probabilistic resource selection functions (RSFs) to predict the potential distribution of dens at the three scales (Jiang et al., 2009). We used a binomial distribution for active natal or resting den presence (1) or absence (0) as the response, with a logit link function in generalized linear models using all possible subsets of covariates (Yang et al., 2018). We used Akaike's information criterion difference corrected for small sample sizes (AICc) and Akaike model weights ( $w_i$ ) to obtain the most parsimonious model (i.e. smallest variables to explain the largest variation, (Buckland et al., 1997; Burnham, 2002), using a threshold of  $\Delta AICc \leq 2$  for each of the three scales. We used the model to predict the probability of den occurrence ( $P_i$ ) in relation to the terrain, vegetation, and anthropogenic variables with binary pika burrow occurrence as the interaction factor (Guo et al., 2017), and further identified the optimal model (and therefore, most significant spatial scale of explanation) using likelihood ratio chi-squared and Wald statistic test in R (both maximum likelihood methods,  $\alpha = 0.05$ ). We used packages *roc*, *lmtest* and *car* (Wikle et al., 2019) and the respective AUC values in these operations (Cherry et al., 2015). We also computed Spearman's-rank correlation coefficient test to check pika burrow occurrence at each plot related with den occurrence probability, modeled at all spatial scales. Additionally, to distinguish the den characteristics, we first excluded inactive dens and their corresponding data from the model due to insufficient encounters. We calculated the difference of the means and descriptive statistics before running the models and one way ANOVA to measure differences between active natal and resting sites. We fixed active natal and resting dens as a dependent and used multiple covariate as independent variables (Rodrick and Mathews, 1999). The regression analysis was computed in R statistical software v 3.5.1 package ([www.r-project.org](http://www.r-project.org), R Core Development Team

2018). Bonferroni Z-statistics to correct for Type 1 error arising from multiple comparisons were performed in SPSS 20.00 (SPSS Inc., and Chicago, Illinois, USA).

### 3. Results

We detected a total of 70 active fox den sites within a total area of 80 km<sup>2</sup>, i.e. 1.3 dens per km<sup>2</sup>. The highest numbers of natal dens were found in bare areas with an intermediate elevation and lowest dens were found in herb patches with low elevation (see Table 1). We encountered maximum resting dens in grass and bare land areas or around rock crevices with intermediate elevation whilst minimum den numbers were detected in shrub patches at the microhabitat scale (Table 1). Rock crevices were not encountered in plantation forest or mixed agricultural land.

#### 3.1. Model selection

We used 17 different subsets of covariates at multiple scales (e.g; landscape scale, six covariates, patch scale; three covariates, microhabitat scale; four covariates and anthropogenic or interaction model; four covariates). We also identified the top nine most parsimonious logistic regression models by considering all resource and human activity variables at the three scales. An interaction term between human activity and pika burrow abundance was additionally retained in each model (Table 2).

#### 3.2. Potential den preference comparisons at multiples scale

At the landscape scale, the most parsimonious resource model included four covariates (elevation, slope, aspect and forest) (no. of model parameters,  $K = 5$ ,  $\hat{\omega} = 0.362$ ; Table 2) and the second most parsimonious resource model additionally incorporated bare ground ( $K = 6$ ,  $\hat{\omega} = 0.062$ ; Table 2). At the landscape scale (Table 2), den occurrence was not well explained by the full suite of covariates ( $AIC_c = 422.87$ , Wald  $\chi^2 = 15.812$ ,  $df = 5$ ,  $t = 5.277$ ,  $p = 0.801$ ,  $AUC = 0.611$ ; Fig. 2a) and showed a weak positive relationship with pika burrow abundance ( $r_s = 0.32$ ,  $df = 6$ ,  $p < 0.014$ ). Elevation was the most significant

**Table 1**

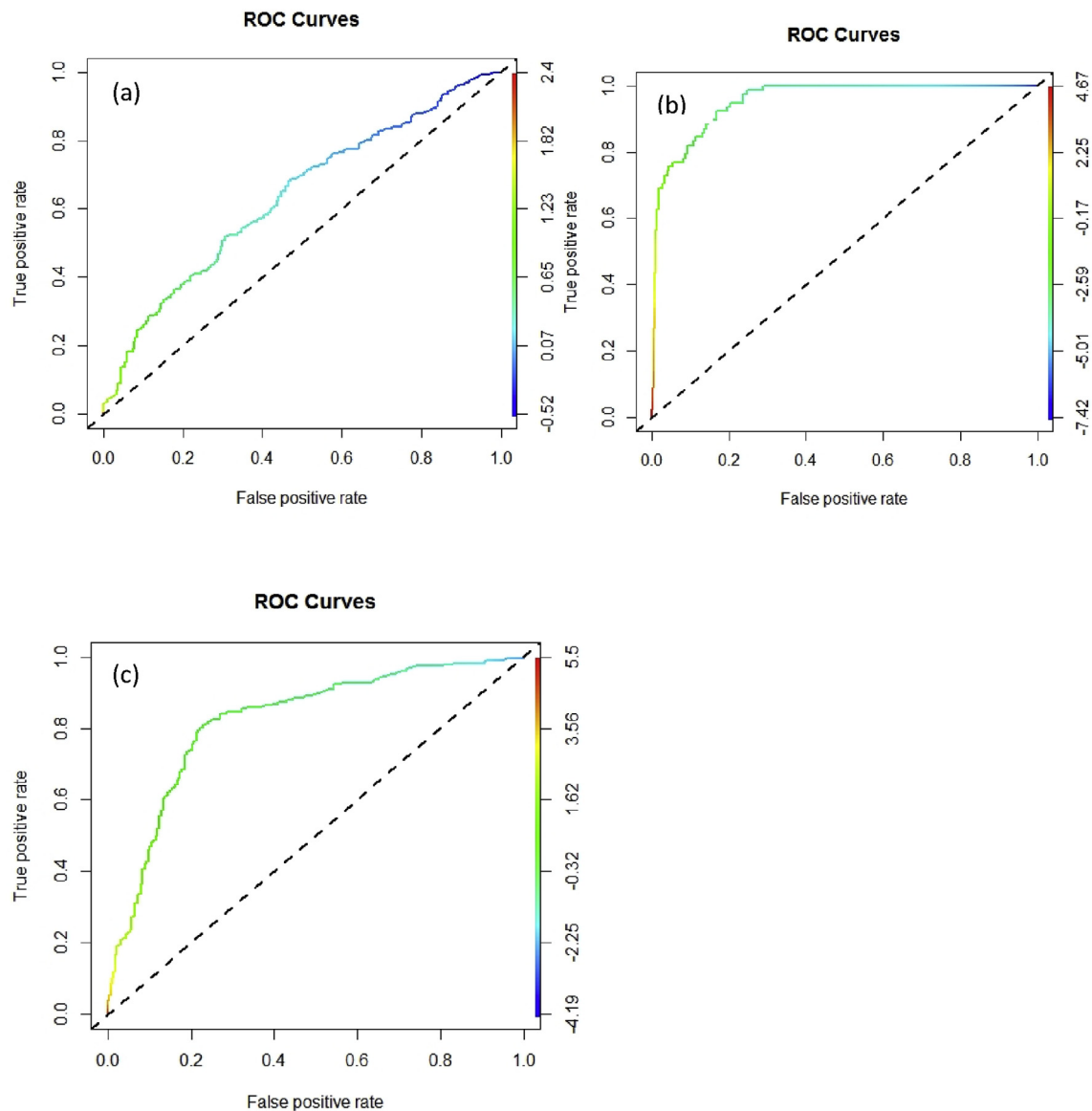
Number of red fox (*Vulpes vulpes montana*) dens of different types (natal/resting) found in different habitat types and elevations, with percentage of the total shown, in the Shigar valley, Karakorum Range, Pakistan.

Den type	Habitat type	Number (%)	Elevation (m)
<b>Natal</b>	Forest patches	6 (25.0%)	2277
	Mixed agriculture land	2 (8.33%)	2232
	Bare area	12 (50.00%)	2875
	Herb patches	2 (4.16%)	2696
	Shrub patches	2 (12.50%)	2424
<b>Resting</b>	Forest patches	2 (14.28%)	2246
	Grass/bare area	20 (83.33%)	2696
	Plantation forests	9 (21.42%)	2131
	Mixed agriculture land	4 (16.66%)	2711
	Shrub patches	3 (7.14%)	2794
	Herb patches	9 (21.42%)	2480

**Table 2**

Number of model parameters (K), differences in Akaike's Information Criterion ( $\Delta AIC_c$ ), and  $AIC_c$  weights ( $w_i$ ) for the most supported logistic regression models (with  $\Delta AIC_c \leq 2$ ) predicting fox den occurrence at three spatial scales in Shigar Valley, Karakoram range, Pakistan.  $w_i$  denotes the importance value index of different vegetation.

Number	Logistic model	k	$AIC_c$	$\Delta AIC_c$	$\hat{\omega}$
<b>Landscape-scale</b>					
1	Den-elevation + slope + aspect + forest	5	422.87	0	0.362
2	Den-elevation + slope + aspect + forest + bare	6	424.37	1.49	0.062
3	Den-elevation + slope + aspect + forest + bare + river	7	425.36	2.49	0.063
<b>Patch-scale</b>					
1	Den-forest patch + shrubs patch	3	420.30	0	0.555
2	Den-forest patch + shrubs patch + herbs patch	4	420.75	0.44	0.444
<b>Microhabitat Scale</b>					
1	Den-n-cover + tree( $w_i$ )	3.	420.92	0	0.46
2	Den-cover + tree( $w_i$ ) + shrubs ( $w_i$ ) + herbs( $w_i$ )	5	421.51	0.58	0.34
3	Den-cover + herbs ( $w_i$ ) + shrubs( $w_i$ ) + tree( $w_i$ )	5	422.84	1.91	0.18
<b>Anthropogenic and interaction model</b>					
1	Den-roads + pika (burrow abundance)	3	385.33	0	0.425
2	Den-agricultural land + roads + pika (burrow abundance)	4	385.36	0.03	0.418
3	Den-agricultural land × pika (burrow abundance) + roads × pika (burrow abundance)	5	387.34	2.01	0.181



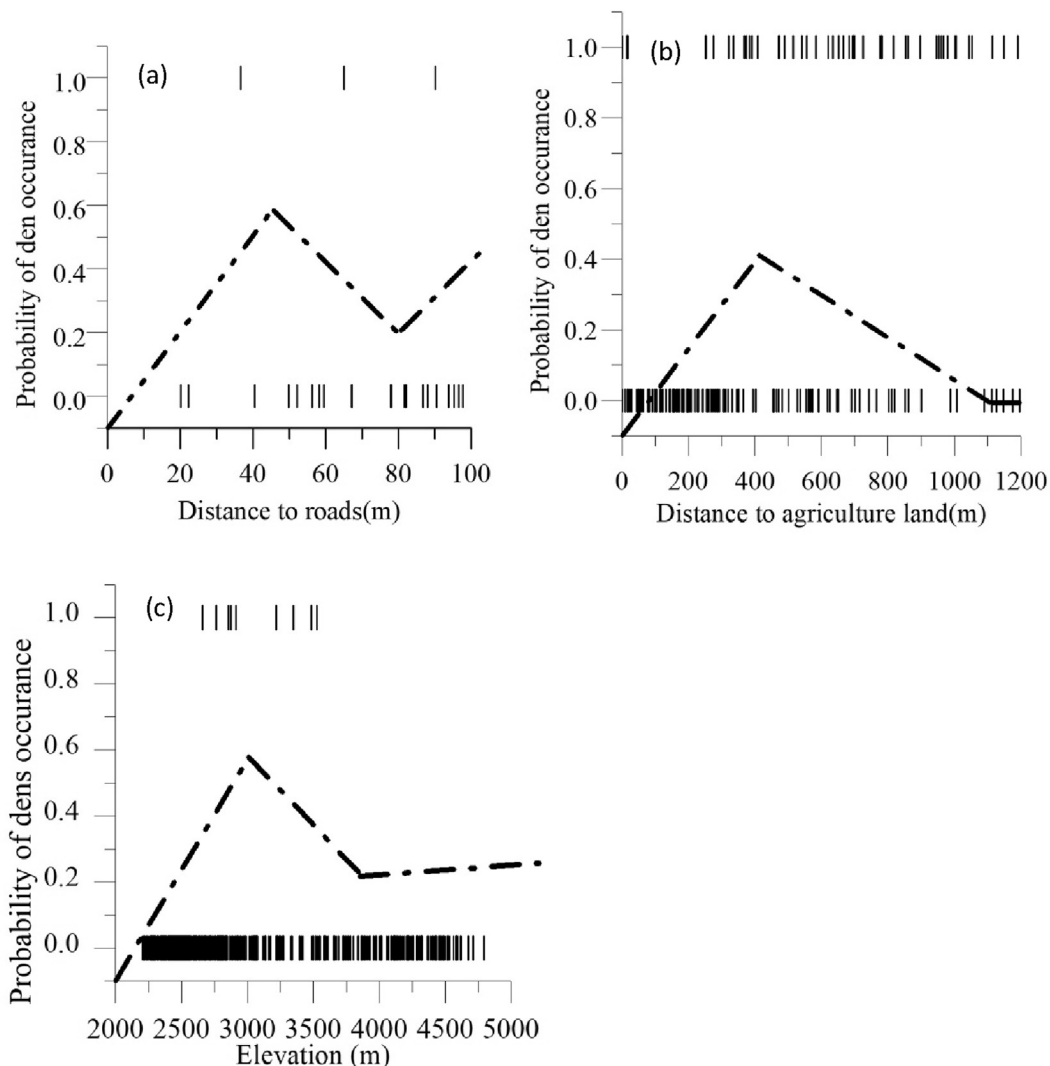
**Fig. 2.** ROC was used to define the accuracy of a classification model at the user-defined threshold value of 0.5 as well as calculated area under the receiver operating characteristic (AUC) curve and derived probabilistic Resource Selection Functions (RSFs) to predict the potential distribution of dens at the three scales (a), landscape (b), patch and (c), microhabitat.

covariate, showing intermediate elevations to be associated with the most fox dens (Fig. 3c). Both slope and forest (including deciduous forest) were negatively related to den occurrence (Table 3). Aspect was non-significant.

At the patch scale, the best resource selection model included two covariates (forest, shrub,  $K = 3$ ,  $\hat{\omega} = 0.555$ ; Table 1) and the second best additionally included herbs ( $K = 4$ ,  $\hat{\omega} = 0.444$ ; Table 1). Den occurrence was best explained by using our full suite of covariates ( $AICc = 420.30$ , Wald  $\chi^2 = 8.228$ ,  $df = 3$ ,  $t = 7.173$ ,  $P < 0.001$ ,  $AUC = 0.912$ ; Fig. 2b; Table 2) with forests being negatively correlated with number of dens and positively correlated with shrubs (Table 3).

At the microhabitat scale, the best resource selection model included two covariates (hiding cover and tree importance value index),  $k = 3$ ,  $\hat{\omega} = 0.46$ ; Table 2), the second-best model incorporated four covariates (cover, tree (ivi), shrubs (ivi) and herbs (ivi),  $K = 5$ ,  $\hat{\omega} = 0.34$ ; Table 2), and the third-best included four covariates (cover, herbs (ivi), shrubs (ivi) and trees (ivi),  $k = 5$ ,  $\hat{\omega} = 0.18$ ; Table 2). At the microhabitat scale, fox den occurrence was poorly explained ( $AICc = 420.92$ , Wald  $\chi^2 = -0.344$ ,  $df = 3$ ,  $t = -0.178$ ,  $P = 0.74$ ,  $AUC = 0.721$ ; Fig. 2c; Table 2). Den occurrence was negatively correlated with hiding cover and positively correlated with tree density (Table 3). Pika burrows and fox dens were positively correlated ( $r_s = 0.513$ ,  $df = 3$ ,  $p < 0.001$ ).





**Fig. 3.** Plots representing the probability of occurrence of dens relative to two types of human disturbance features (a, b) and one type of landscape covariates (c), in Shigar valley, Karakorum range. Fox den occurrence was allowed to vary with distance from disturbance features while other covariates were held at their mean values of den at landscape scales.

For the models containing anthropogenic factors and interactions terms, the best model consisted of two covariates (distance to roads and pika burrow occurrence,  $k = 3$ ,  $\omega = 0.425$ ; Table 2), and the second-best included three covariates (distance to agricultural land, distance to roads, and pika burrow abundance,  $k = 4$ ,  $\omega = 0.418$ ; Tables 2 and 3; Fig. 3b). The best model performed at an intermediate level for explaining fox den occurrence ( $AICc = 385.33$ , Wald  $\chi^2 = 9.238$ ,  $df = 3$ ,  $t = 8.864$ ,  $P < 0.001$ ,  $AUC = 0.721$ ). Den occurrence was negatively correlated with distance to roads (Fig. 3a) and positively correlated with pika burrow occurrence (Table 3). Overall, the best models were all at patch scale: models at microhabitat scale were intermediate; and models at the landscape scale were poor. Pika burrow occurrence was higher along the quieter roads (little traffic volume), and in bare and rocky areas.

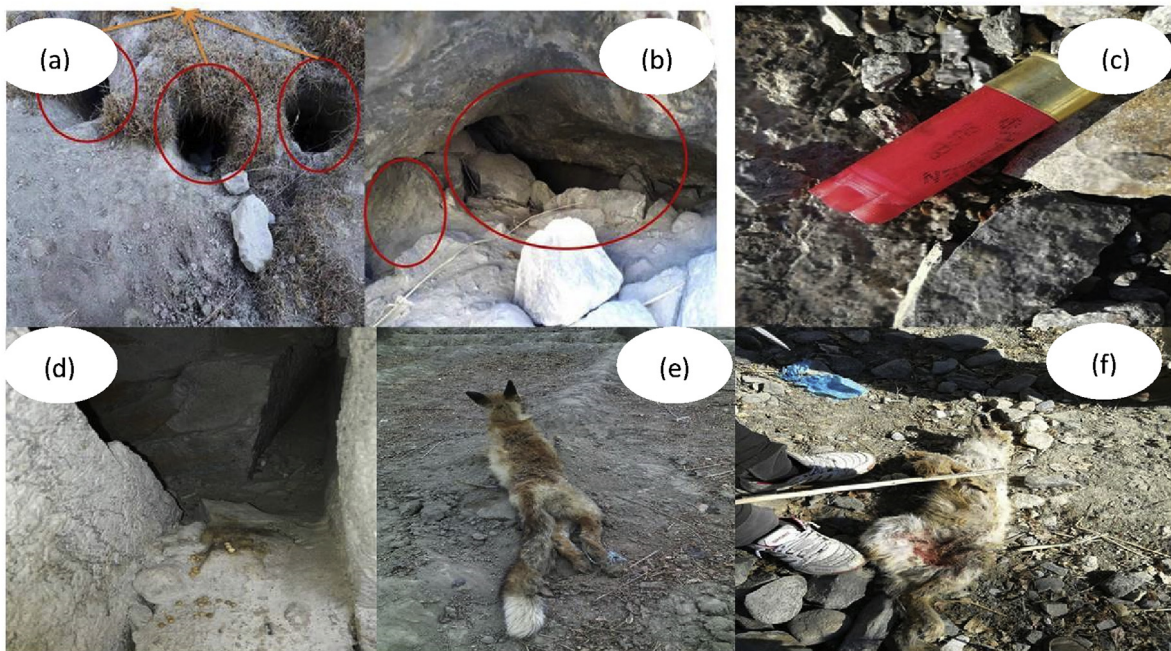
### 3.3. Den characteristics

We found that den entrance size was greater for natal dens than resting dens (Fig. 4 a & b; Table 4). However, in areas with high mean den widths, significantly fewer natal dens were observed (Table 4). Natal den depth was greater than resting den depth (Table 4). Furthermore, the number of openings was greater for natal dens than for resting ones (Table 4). Temperature oscillations inside natal and resting dens were not statistically different (Table 4).

**Table 3**

Best-fit logistic regression model predicting fox den site distribution in the Shigar Valley, Karakoram range, North-west Pakistan at landscape, patch, and microhabitat scales. Asterisks mark the 95% confidence intervals that do not include 0.

Variable	Coeff	S.E.	95% CL
<b>Landscape</b>			
Intercept	2.326	0.156	2.016 to 2.633
Elevation	0.780	0.106	0.581 to 1.000
Slope	-0.446	0.140	-0.721 to -0.170
Aspect	-0.045	0.136	-0.310 to 0.220
Forest	-0.420	0.124	-0.665 to -0.174
<b>Patch</b>			
Intercept	-3.015	0.161	-3.337 to -2.696
Forest	-0.753	0.105	-0.961 to -0.544
Shrub	0.532	0.121	0.284 to 0.802
<b>Microhabitat</b>			
Intercept	-0.676	0.142	-0.954 to -0.387
Cover	-0.674	0.111	-0.893 to -0.455
Tree	0.326	0.151	0.011 to 0.642
<b>Anthropogenic</b>			
Intercept	-1.228	0.124	-1.352 to -0.865
Roads	-0.362	0.108	-0.563 to -0.165
Pika burrows	0.552	0.312	0.176 to 0.052



**Fig. 4.** Examples of earthen multiple entrance dens and non-earthen dens located during the study (a), grass dominated land (b), hanging rocks crevices in the bare area of Shigar valley and the red circles identify entrance position as well as footprints was also prominent on the substrates (c), Bullet recorded after shooting (d), Pika active burrow in the rock crevices with had a fresh fecal pellets (e), adult male specimen of fox killed by poison (f), a subadult vixen shot by villagers. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

## 4. Discussion

### 4.1. Multiple-scale resource selection

Our results reflect the generalist nature of the red fox in that landscape scale (2nd order) selection was characterized by a general preference for broad topographical features rather than specific habitats, aside from a propensity to avoid very closed habitats i.e. forest. However, foxes did not appear to avoid human activity, although the relationship was non-linear. Dens were associated with high prey (pika) occurrence. Further, one of the topographical features – elevation – may have been confounded by human activity because most villages were sited at low elevations. Pika burrow abundance was also low in forest compared to bare habitat with some rocky and grassy areas. In these areas dry grasses, herbs and twigs provided food

**Table 4**

Differences in physical characteristics between natal and resting dens of red fox (*Vulpes vulpes montana*), and their comparison using one-way analysis of variance (ANOVA). Standard error means differences were calculated for each den characteristic.

Den characteristics	Resting (n = 42)	Natal (n = 28)	Df	F	Sig.
Entrance diameter (cm)	43.90 ± 18.41	93.89 ± 99.04	122	10.240	0.002
Width (cm)	50.17 ± 28.31	107.68 ± 96.90	105	13.194	0.001
Depth (cm)	110.05 ± 105.80	169.11 ± 124.139	80	4.554	0.036
Number of openings	1.93 ± 1.237	2.24 ± 1.628	75	4.088	0.047
Temperature (°C)	13.76 ± 4.943	13.75 ± 3.087	96	0.020	0.991

resources for pika in both summer and winter. Prey, i.e. pika occurrence is likely to be a factor explaining the positive association between fox dens and bare habitat as at least in part foxes selected terrain because it contained prey. This is consistent with another study on fox den site selection albeit in the very different environment of the Canadian Arctic (Gallant et al., 2014) where foxes primarily selected den sites based on prey richness. Further (Márton et al., 2016), report that both foxes and Eurasian badger (*Meles meles*) establish dens/setts near rodent burrows. The Indian pika is a diurnal species that does not hibernate during harsh winters (Upadhyay and Bahuguna, 2013), and is thus a year-round dietary item for foxes.

At the patch scale, foxes selected shrubs and, again, avoided forests. The findings corroborate those for a congeneric species in a similar environment - Tibetan fox (*V. ferrilata*) in China, which was found to prefer shrub grassland over forests (Wang et al., 2008). It is likely that this preference represents a compromise between areas that contain an abundance of prey, and the availability of some cover for protection from predators. Both Tibetan foxes and red foxes may be preyed upon by wolves (*Canis lupus*) and persecuted by humans (Wikenros et al., 2017) hence behaviour that reduces exposure to these two factors will likely enhance fitness. At the patch scale, pika abundance did not significantly affect den occurrence, which is surprising given its importance at the 2nd and 4th order (landscape and microhabitat level). The effect of fuelwood cutting in forest plantation patches represents a risk to fox cubs as dens can be exposed during this process, potentially reducing cub survival. Therefore, forest cover may be selected against partly as an artefact of avoiding human activity, and partly because foxes are better hunters in open habitats (Zaman et al., 2020). At the microhabitat scale, tree habitats (ivi) were most preferred and pika occurrence strongly affected den occurrence. These findings are consistent with Punjabi et al. (2013) who also report that at the microhabitat scale, rodent abundance and visibility determined fox den site selection. The association of red fox dens with high shrub density and fruiting shrubs in particular, is consistent with Rosalino et al. (2010), who report that several species of carnivores, including the red fox, are important seed germinators and dispersers, as are pikas (Bhattacharyya et al., 2013).

Other studies found that foxes hunted near roadsides at night, possibly as a strategy for avoiding competition with sympatric weasels (e.g., Bhatia et al., 2017), or because roads provide food in the form of road-killed carrion. Many carnivore species, including Tibetan foxes, use road sides for opportunistically scavenged carrion (Vanak and Gompper, 2009) and this behavior may explain the non-linear relationship between fox den occurrence and roads in our study. Dens near roads may therefore function as escape routes when foxes are exploiting food resources in these areas.

#### 4.2. Den characteristics

The disproportionate number of openings found in natal dens has also been reported in other fox species, and it is suggested that a proliferation of openings may signify permanent or semi-permanent den sites (Reshamwala et al., 2018). We found that foxes commonly utilized natural rock crevices and sunbathed or rested in association with sea buckthorn (*Hippophaes rhamnoides*) vegetation, presumably to reduce the energetic cost of digging, and dug dens only when no such structures were accessible (Stanley, 1963). Home and Jhala (2010) reported that foxes may use single or multiple breeding dens during the breeding season, potentially to confuse predators.

## 5. Conclusions

We show that foxes did not completely avoid human activity, which may in part relate to resource exploitation, and foxes selected dens sites closer to pika burrows than would be expected from a random distribution. This study forms a baseline from which to further explore predator-prey interactions in an under-studied region. Foxes focus their activities near den sites throughout the breeding season and frequently visit dens at other times of the year, hence den site selection is an important consideration for fox management and conservation.

### Ethical approval

**All applicable international**, national and/or institutional guidelines for the care and use of animals were followed. We conducted this observational and non-invasive study according to the regulations for animal welfare and conservation under the Gilgit- Baltistan Wildlife Preservation Act 1975 and the Northeast Forestry University Guidelines for the Use of Animals in Research.

## Author contributions

GJ designed and supervised this research work, including statically analysis and scale design. MZ did the fieldwork and is the writer of this manuscript, B.T. reviewed and edited the manuscript throughout, MYZ contributed in the design of the manuscript.

## Declaration of competing interest

The authors declare that they have no conflict of interest.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01136>.

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Macdonald, 1983; Saunders et al., 1995; Tannerfeldt et al., 2003; Weston et al., 2012.

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