

Original Article

# Seasonal resource selection of an arboreal habitat specialist in a human-dominated landscape: a case study using red panda

Damber BISTA <sup>a,\*</sup>, Greg S. BAXTER<sup>b</sup>, Nicholas J. HUDSON<sup>a</sup>, and Peter J. MURRAY<sup>b</sup>

<sup>a</sup>School of Agriculture and Food Sciences (Wildlife Science Unit), The University of Queensland, Gatton, QLD 4343, Australia and <sup>b</sup>School of Agriculture and Environmental Science, University of Southern Queensland, Darling Heights, QLD 4350, Australia

\*Address correspondence to Damber Bista. E-mail: d.bista@uqconnect.edu.au.

Handling Editor: Zhi-Yun Jia

Received on 19 October 2021; accepted on 24 February 2022

## Abstract

Human-dominated landscapes provide heterogeneous wildlife habitat. Conservation of habitat specialists, like red pandas *Ailurus fulgens*, inhabiting such landscapes is challenging. Therefore, information on resource use across spatial and temporal scales could enable informed-decision making with better conservation outcomes. We aimed to examine the effect of geo-physical, vegetation, and disturbance variables on fine-scale habitat selection of red pandas in one such landscape. We equipped 10 red pandas with GPS collars in eastern Nepal in 2019 and monitored them for 1 year. Our analysis was based on a generalized-linear-mixed model. We found the combined effect of geo-physical, vegetation, and disturbance variables resulted in differences in resource selection of red pandas and that the degree of response to these variables varied across seasons. Human disturbances, especially road and cattle herding activities, affected habitat utilization throughout the year whereas other variables were important only during restricted periods. For instance, geo-physical variables were influential in the premating and cub-rearing seasons while vegetation variables were important in all seasons other than premating. Red pandas selected steeper slopes with high solar insolation in the premating season while they occupied elevated areas and preferred specific aspects in the cub-rearing season. Furthermore, the utilized areas had tall bamboo in the birthing and cub-rearing seasons while they also preferred diverse tree species and high shrub cover in the latter. Our study demonstrates the significance of season-specific management, suggests the importance of specific types of vegetation during biologically crucial periods, and emphasizes the necessity to minimize disturbances throughout the year.

**Key words:** *Ailurus fulgens*, anthropogenic disturbances, habitat specialists, habitat utilization, resource use, spatio-temporal variation, vegetation

Habitat selection is a multi-scale process (Johnson 1980) which is determined by many factors. For example, quality and quantity of forage, cover availability, access to water, resting and nesting sites, predator avoidance, and fulfillment of other life history needs (Manly

et al. 2002; Bonnot et al. 2015). Ecological theories suggest that species are guided by the cost and benefit of using available habitat. For that reason, the resource selection patterns of an individual animal vary in response to seasonal changes in environmental conditions,

habitat characteristics, and biological requirements over the annual cycle (Pyke 1984; Bonnot et al. 2015; Michel et al. 2018).

Spatial and temporal variation in resource selection patterns is more obvious in areas with high seasonality (Lowrey et al. 2017; Williams et al. 2017). For instance, the availability and quality of forage differ across seasons (Smolko et al. 2018; Zhang et al. 2018). Herbivores experience high predation risk (Lendrum et al. 2018; Peers et al. 2020), low forage availability (DelGiudice et al. 2013; Seto et al. 2015), and high movement cost (Pedersen et al. 2021; Sheppard et al. 2021) when the habitat is covered with snow. Furthermore, they require specific environments for different activities which influence their seasonal habitat selection (Krausman 1999; Michel et al. 2018). For example, mothers with dependent young exhibit risk aversion as they are concerned with the safety of their offspring (Brown et al. 1999; Sergio et al. 2007), while they can be risk prone when they are alone, especially during the mating season (Edomwande and Barbosa 2020). The perceived level of disturbances by wildlife also varies with the intensity of human activities (Eldegard et al. 2012).

Increasing human activities are transforming wildlife habitat and can increase the risk of extinction (Haddad et al. 2015). Availability of resources and the potential risk of obtaining them differ on spatial and temporal scales and this drives disproportionate use of habitat (Blecha et al. 2018; William et al. 2018). Nevertheless, some species inhabiting modified landscapes can adapt through behavioral plasticity and habitat selectivity (Crooks 2002; Tucker et al. 2021). To adapt in such landscapes, individuals partition their activity (Hebblewhite and Merrill 2007; Wevers et al. 2020), occupy high-quality patches (Martin et al. 2010) and avoid disturbances (Hebblewhite and Merrill 2007; Graham et al. 2009). These behaviors have direct implications for survival in human-modified habitat as the cost of searching and escape are inflated in heterogeneous habitat, ultimately affecting the fitness of the animal (Rosenzweig 1981). One concern is that habitat specialists could be more vulnerable in these circumstances (Pfeifer et al. 2017; Tucker et al. 2018). Failure to adapt can affect fitness and population dynamics, which can ultimately result in local extirpation of a species (Crooks 2002; Haddad et al. 2015). This raises the need to understand how a habitat specialist utilizes habitat at a fine scale and how they obtain sufficient resources in modified landscapes. We, therefore, report the seasonal resource selection patterns of the red panda *Ailurus fulgens*, an arboreal habitat specialist of the Eastern Himalaya.

The red panda is a medium-sized endangered mammal inhabiting temperate forests above 2,300 m (Glatston et al. 2015). This species relies nearly exclusively on bamboo leaves and shoots (Yonzon and Hunter 1991; Zhang et al. 2009; Bista et al. 2022b). They are solitary and territorial except during the breeding season and when the mother is raising her cubs (Yonzon 1989; Bista et al. 2022a). This species is under threat due to habitat loss and fragmentation throughout their range (Dalui et al. 2020; Hu et al. 2020). Nearly half of their population has been reported to have extirpated in the last 20 years (Glatston et al. 2015). Human activities, especially road construction, hydro-power projects, electric transmission lines, livestock herding, and habitat encroachment for farming and settlement are the leading drivers of these losses (Acharya et al. 2018; Panthi et al. 2019; Dendup et al. 2020). Some of the remaining populations are surviving in fragmented habitat amidst increasing human pressure which leaves them even more vulnerable (Thapa et al. 2018; Dalui et al. 2020). This overall reduction in population indicates the insufficiency and ineffectiveness of existing conservation programs.

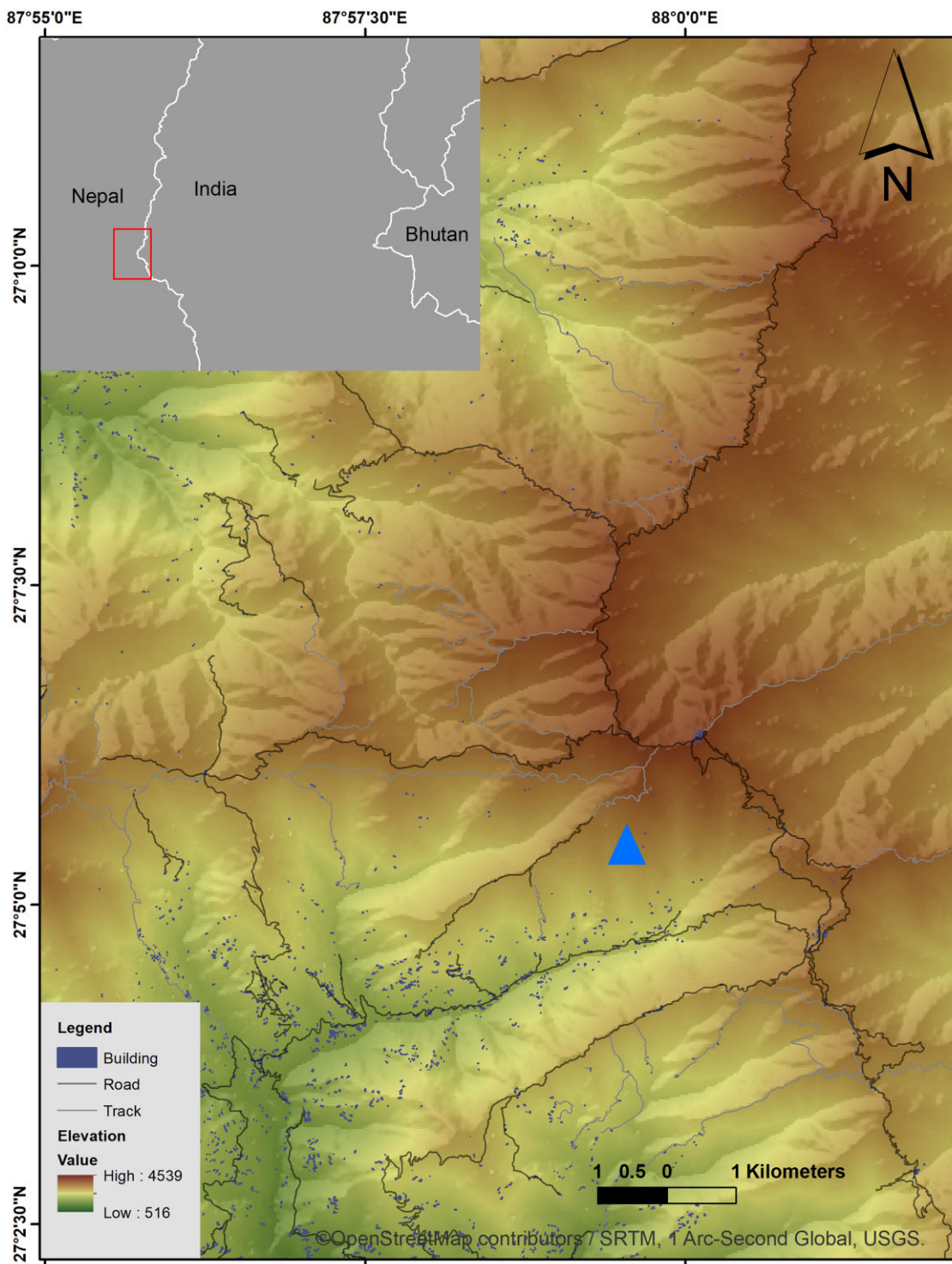
The majority of studies on resource selection of red pandas have reported vegetation factors, such as canopy cover (Pradhan et al. 2001; Williams 2006; Bista et al. 2019), bamboo cover (Pradhan et al. 2001; Zhang et al. 2004; Dorji et al. 2011), bamboo height (Pradhan et al. 2001; Zhang et al. 2004; Dorji et al. 2011), tree size (Williams 2006; Dorji et al. 2011; Bista et al. 2019), shrub cover (Wei et al. 2000), species richness (Bista et al. 2019), and food resources (Zhang et al. 2009) as the major determinants of resource selection. Some studies have also documented the role of geo-physical variables, such as elevation (Yonzon and Hunter 1991; Thapa et al. 2020), distance to water sources (Yonzon and Hunter 1991; Pradhan et al. 2001; Dorji et al. 2011; Bista et al. 2019), aspect (Yonzon et al. 1991; Dorji et al. 2011; Bista et al. 2017), and slope (Wei et al. 2000; Dorji et al. 2011; Bista et al. 2017). Those studies have been instrumental in understanding the ecology of this species in natural habitat and this has contributed to their conservation to some extent. Yet we lack detailed information on how this species responds to disturbances, and geo-physical, and vegetation-related factors on seasonal scales.

The major objective of this study was to evaluate the roles of geo-physical, vegetation, and disturbance covariates on seasonal resource selection patterns of red pandas in a human-dominated landscape. Given their low ecological plasticity, and seasonal variation in movement (Yonzon 1989; Reid et al. 1991; Zhang et al. 2009; Bista et al. 2021b) and space use patterns (Yonzon 1989; Reid et al. 1991; Bista et al. 2022a), we hypothesized a different degree of response to geo-physical, vegetation, and disturbance variables across seasons. We predicted that vegetation-related variables would be more important determinants of habitat utilization than geo-physical variables (such as elevation, aspect, slope, topographic position index [TPI], solar radiation, and water). Second, we predicted that red pandas avoid disturbances, such as roads (Qi et al. 2009), cattle herding stations (Fox et al. 1996; Williams 2006; Sharma et al. 2014; Dendup et al. 2017; Acharya et al. 2018), and walking tracks (Acharya et al. 2018; Panthi et al. 2019). Moreover, as a male shares the home range of several females, and females provide parental care, and live with their dependents for 7–8 months (Yonzon 1989; Bista et al. 2022a), we hypothesized that females are more selective in habitat utilization than males.

## Material and Methods

### Study site

Our study area was in Ilam and Panchthar districts, eastern Nepal (Figure 1). This area has a sub-tropical and temperate climate with a mean annual temperature of 13.1 °C (SD 6.78, range –1 to 28.9 °C). Annual precipitation was 2,590 mm with nearly 80% in the monsoon from June to September (Subba et al. 2019). Elevation ranges from 2,000 to 3,636 m with higher elevations in the north. This area has sub-tropical and temperate broad-leaved mixed and deciduous forests with bamboo in the understorey. Most of the deciduous trees, such as *Sorbus cuspidata*, *Lyonia ovalifolia*, *Hymenodictyon excelsum*, *Betula utilis*, *Acer campbellii*, *Magnolia* spp., and *Actinidia callosa* shed their leaves during the winter. The study area supports grazing of livestock such as yaks, cows, and goats throughout the year. However, some herders follow a transhumance herding regime whereby they move with their livestock to high elevations (3,128 ± 300 m) in the summer where they stay for 8–9 months (March–November) and move to lower elevation in the winter (2,811 ± 126 m). Most settlements are in lower elevations



**Figure 1.** Map of the study area in Ilam and Panchthar districts in eastern Nepal which borders with India in the east (as shown in inset with red rectangle) where elevation ranged from 1,500 to 3,636 m. Blue triangle shows the animal capture site.

(~2,600 m), where human activities are relatively higher than in high elevation.

#### Data collection and processing

We captured 10 red pandas (6 females and 4 males) using a cage trap and equipped them with GPS collars (LiteTrack Iridium 150 TRD) following a standard protocol (Bista et al. 2021c). We

collared these animals from September to December 2019 and monitored them until March 2021. These collars ranged from 224 to 229 g which was just over 6% of the body weight of a typical adult. Three animals were sub-adults when collared (2 females and 1 male). However, we included these sub-adults in analyses only when they started living independently in a new home range after dispersal (details in Bista et al. 2022a). Additionally, we excluded animals

having less than 25 fixes to minimize bias due to sample size variation. This also allowed us to retain a minimal sample size of 5 required for running mixed models across seasons (Harrison 2015).

The GPS collars recorded one fix every 2 h. Our study area had dense forest canopy and rugged terrain which can reduce the chances of obtaining successful GPS (Robert et al. 2002; Hebblewhite et al. 2007; Hansen and Riggs 2008). To minimize the telemetry error, we retained valid GPS fixes by omitting those with  $\leq 2$  satellites and dilution of precision  $> 5$  (Lewis et al. 2007). Furthermore, we excluded the first week's data from each animal to minimize the effect of behavioral disruption resulting from capturing and collaring them. We found empirically that our collars had telemetry errors up to 25 m.

To collect data on habitat variables, we conducted surveys in 4 seasons based on red panda biology: premating (November–December), mating (January–March), gestation and birthing (April–July), and cub rearing (August–October; Supplementary Figure S1). Red pandas breed in the winter, and their birthing and cub-rearing seasons overlap with the monsoon.

We considered the resource selection pattern within the home range of each animal as our study scale (Johnson 1980). Initially, we demarcated the seasonal home range of each individual as a weighted autocorrelated kernel density estimation at the 95% isopleth in the cmm package (Fleming and Clalabrese 2021), see detail in Bista et al. (2022a). Then we overlaid grids ( $250 \times 250$  m) in those home ranges and covered over 80% of those total grid points within each animal's home range. We could not access the remaining grids due to the inaccessibility of the terrain. We collected vegetation data (Table 1 and Supplementary Figure S2) from the centroid of these grids where we set up a circular concentric plot of 10 m radius for trees, 3 m radius for shrubs, and 1 m radius for bamboo (Bista et al. 2017; Acharya et al. 2018). We also established 4 additional plots of 1 m radius at the outskirts of each 10 m plot, each 2 m away from the boundary in each of the 4 cardinal directions (east, south, west, and north) to optimize the bamboo data. The minimum distance between 2 consecutive plots was 250 m to ensure spatial independence.

To evaluate the effect of vegetation productivity on resource selection, we included the Normalized Difference Vegetation Index (NDVI) as a measure of productivity and greenness of the sampling grids. We obtained the composite layers of NDVI at 250 m resolution (MOD13Q1-v006, 16-Day) of the study period for each season from the US Geological Survey (USGS) earth data.

We included 6 geo-physical variables which comprised elevation, slope, aspect, TPI, solar radiation, and distance to water (Table 1 and Supplementary Figure S2). We obtained the Global Digital Elevation Model (DEM, Shuttle Radar Topography Mission, 1 arc-second) from the USGS and extracted elevation, aspect, slope, and TPI of the sampling plots. To measure the use of landform types, we used TPI. Low TPI values represent valleys while high values indicated elevated areas such as ridges (De Reu et al. 2013). We included solar radiation as a measure of the effect of temperature on seasonal habitat use (Allen et al. 2015) and prepared solar radiation maps of the study area from the DEM for each season. Using the DEM, we developed a watershed map of the study area for dry (November–April) and wet seasons (May–October). Then we verified the watershed map through physical survey and consultation with local people and extracted the distance between each sampling plot and the nearest water source.

Disturbance covariates included distance to road, human-walking track, cattle station, and settlement (Table 1 and Supplementary Figure S2). We recorded the GPS locations of each

cattle station and settlements within the study area and accessed road and walking track data from Open Street Map and verified the data through physical survey. We estimated Euclidean distance between the centroid of each grid and these features. The total presence records of each red panda falling within all grids was computed using the join and relate tool in ArcGIS version 10.8 (ESRI 2020). We assigned the count value as 0 for grids having no presence records.

### Data analyses

We checked multicollinearity (excluding sex, Table 1) using the generalized variation inflation factor and we retained variables with  $\text{GVIF}^{1/2 \times df} \leq 2$  for further analyses (Fox and Monette 1992). Autocorrelation is quite common in satellite telemetry data (Koper and Manseau 2012). Therefore, we employed a generalized linear mixed model for further analyses as this is one of the best approaches to compute resource selection in autocorrelated telemetry data if the response variable has count data (Bolker et al. 2009; Koper and Manseau 2012). We centered and scaled all the continuous variables to maintain consistency (Harrison et al. 2018). We considered the total number of presence records within each grid as the response variable and included individual identity of animals as a random factor and predictors as fixed factors.

Initially, we ran the global model with the Poisson family, but all resulting models suffered from overdispersion and zero inflation. Therefore, we ran models with the negative-binomial family using zero-inflation in the glmmTMB package (Brooks et al. 2017). Then we fitted the resource selection function with maximum-likelihood estimation and Laplace approximation. We followed the backward stepwise procedure to obtain the best set of candidate models and selected the final model based on the corrected Akaike's Information Criterion (AICc). Then we averaged models if  $> 1$  model was within  $\Delta\text{AICc} < 2$  (Burnham et al. 2011).

We categorized grids into either selected or available, based on the presence records. The former having presence records while the latter had zero presence. Using 1-sample *t*-tests, we examined the differences between solar radiation, bamboo height, and bamboo cover in selected and available aspects. We also examined the variation represented by the fixed and random effects with marginal and conditional  $R^2$  values (Nakagawa and Schielzeth 2013). The former represents variation represented by the fixed effects while the latter accounts for the variation represented by both fixed and random effects. We evaluated the intra-seasonal difference in elevation use using Kruskal–Wallis rank-sum test and performed post-hoc Dunn test to compare pair-wise differences.

We used *k*-fold cross validation for evaluating model performance. First, we split the data into 5 folds and generated 10 equal-size bins for each fold (Roberts et al. 2017). Then we summed the presence counts in each bin, estimated area-adjusted frequency, and ranked bins from low to high probability of resource selection. Finally, we computed the correlation between area-adjusted frequency and the bin rank using Spearman's rank correlation (Boyce et al. 2002). A strong correlation was regarded as evidence of good predictive performance of a model (Boyce et al. 2002). We repeated this process for all seasons.

### Results

We recorded 14,111 GPS fixes from 10 red pandas over 490 days. After omitting erroneous fixes, we retained 7,245 relocations. On average we recorded a median of 212 fixes (range 27–730) from

**Table 1** Description of variables included in the study

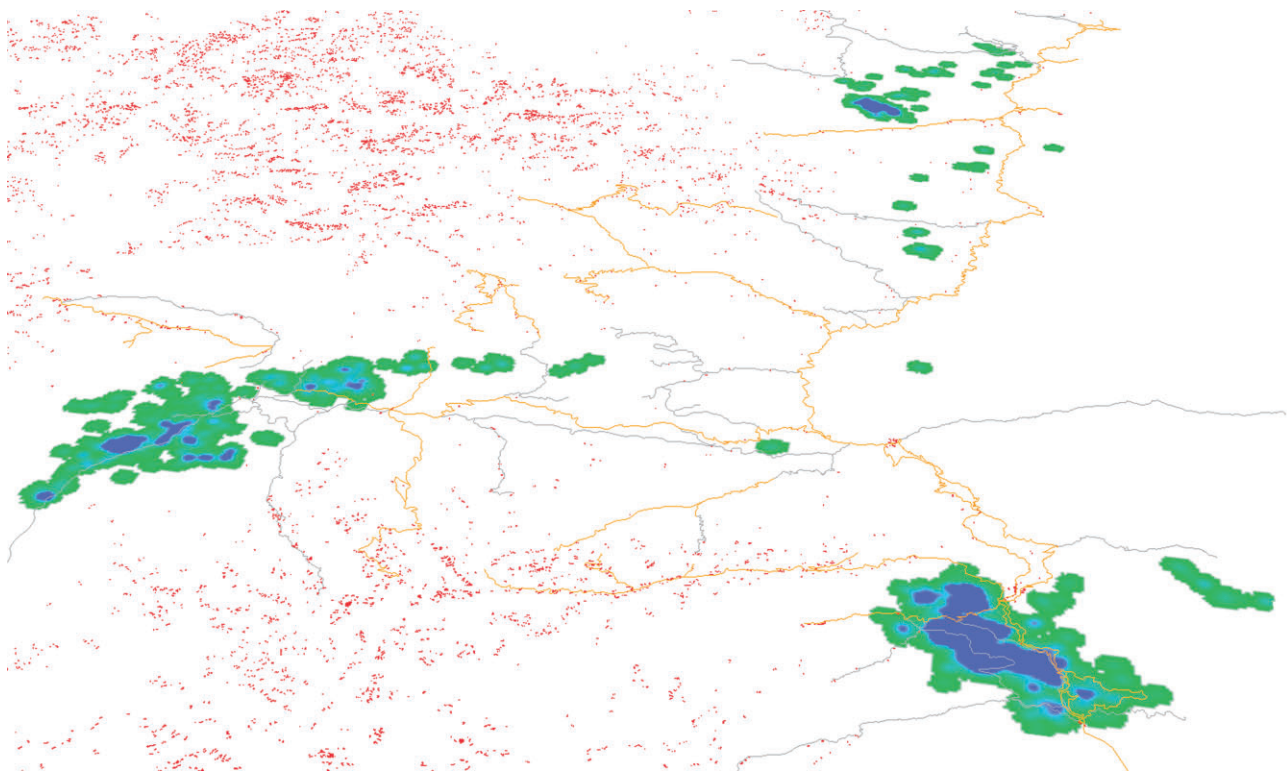
Variables	Description	Range
Sex	Sex of study animals	Male, female
Count	Number of locations visited in a grid per individual	0–329
Geo-physical variables		
Elev	Elevation of sampling grid in m a.s.l. Source: Shuttle Radar Topography Mission (SRTM, 1 arc-second) Global DEM— <a href="https://earthexplorer.usgs.gov/">https://earthexplorer.usgs.gov/</a>	2,404–3,225 m
Aspect	Aspect of sampling grid categorized into 8 cardinal directions. Source: SRTM, 1 arc-second DEM— <a href="https://earthexplorer.usgs.gov/">https://earthexplorer.usgs.gov/</a>	East (E), North (N), Northeast (NE), Northwest (NW), South (S), Southeast (SE), Southwest (SW), West (W)
Slop	Slope of sampling grid (°). Source: Shuttle Radar Topography Mission (SRTM, 1 arc-second). Source: SRTM, 1 arc-second DEM— <a href="https://earthexplorer.usgs.gov/">https://earthexplorer.usgs.gov/</a>	2–52°
Sola	Solar radiation received in a sampling grid (KW/m <sup>2</sup> ). We obtained the incoming solar radiation from the DEM (SRTM, 1 arc-second) using area solar radiation tool in ArcMap. Source: SRTM, 1 arc-second DEM— <a href="https://earthexplorer.usgs.gov/">https://earthexplorer.usgs.gov/</a>	3.3–908.4 KW/m <sup>2</sup>
TPI	TPI of sampling grid. The high value and low value represent ridge and valley areas, respectively. Source: SRTM, 1 arc-second DEM— <a href="https://earthexplorer.usgs.gov/">https://earthexplorer.usgs.gov/</a>	–23.6 to 20.5
Wat_dis	Euclidian distance between a sampling plot and the nearest water source (m).	0–303 m
Vegetation variables		
NDVI	NDVI of the sampling grid. MOD13Q1 v006 16-Day 250 m NDVI product. Source: <a href="https://earthexplorer.usgs.gov/">https://earthexplorer.usgs.gov/</a>	0.05–0.94
Tree_cov	Average canopy of trees within a plot based on visual estimation (%).	0–92%
Tre_dbh	Diameter at breast height of tree. Threshold: 1.3 m tall to be a tree.	0.67–525.6 m
Tre_rich	Tree richness in sampling grid. Species richness = $S/(\sqrt{N})$ , where $S$ = number of species and $N$ = total number of individuals (Menhinick 1964).	0–2.2
Tre_fir	Average height of first branch of trees above the ground within the plot (m).	0.16–33 m
Shu_cover	Area covered by shrubs based on visual estimation within the plot (%).	0–8.5%
Bam_cov	Area covered by bamboo based on visual estimation within 5 plots (%).	0–100%
Bam_hei	Average height of bamboo culm in sampling grid (m)	0.1–11.4 m
Disturbance variables		
Catt_dis	Distance between the center of a sampling grid and the nearest cattle station (m).	30–2,547 m
Trac_dist	Distance between the center of a sampling grid and the nearest human-walking track (m): Source: <a href="https://www.openstreetmap.org/">https://www.openstreetmap.org/</a>	0–2,066 m
Road_dist	Distance between the center of a sampling grid and the nearest road (m). Source: <a href="https://www.openstreetmap.org/">https://www.openstreetmap.org/</a>	0–2,477 m
Sett_dist	Distance between the center of a sampling plot and outskirts of the nearest settlement (m).	30–3,153 m

each animal per season (details in [Supplementary Table S1](#)). We surveyed 522 grids throughout the year with an average of 130 grids per season (range 84–195). Nearly 70% of these grids ( $n = 362$ ) had presence records which clearly shows disproportional habitat use ([Figure 2](#) and [Supplementary Figure S3A–D](#)). Each presence grid had a median of 9 fixes (interquartile range 2–25, maximum 329).

There was variation in red panda resource selection across seasons. The averaged model for the pre-mating season included elevation, slope, solar radiation, distance to water source, roads, and cattle stations ([Table 2](#)). Red pandas strongly avoided areas close to roads ( $\beta = 1.34$ ,  $P < 0.003$ , [Figure 3A](#)) and marginally stayed away from cattle stations ( $\beta = 0.8$ ,  $P = 0.07$ , [Figure 3C](#)). The intensity of habitat use appeared to be high in low elevation ( $\beta = -0.7$ ,  $P < 0.03$ , [Figure 3J](#)) in areas with steeper slopes ( $\beta = 0.3$ ,  $P = 0.05$ , [Figure 3K](#)) and where the solar insolation was high ( $\beta = 1.03$ ,  $P < 0.001$ , [Figure 3L](#)).

The selected model for the mating season included sex, NDVI, tree cover, shrub cover, bamboo cover, and distance to cattle stations and human-walking tracks ([Table 2](#)). Red pandas showed negative responses to NDVI ( $\beta = -0.44$ ,  $P < 0.04$ , [Figure 3D](#)) and shrub cover ( $\beta = -0.45$ ,  $P < 0.006$ , [Figure 3H](#)) while they exhibited affinity for bamboo cover although this was not significant ([Supplementary Table S2](#)). They avoided cattle stations ( $\beta = 0.39$ ,  $P < 0.04$ , [Figure 3C](#)) but showed affinity to areas close to human-walking tracks ( $\beta = -0.52$ ,  $P < 0.004$ , [Figure 3B](#)).

The averaged model for the birthing season included TPI, NDVI, tree cover, bamboo height, and distance to cattle stations and human-walking tracks ([Table 2](#)). Red pandas avoided cattle stations ( $\beta = 0.67$ ,  $P < 0.001$ , [Figure 3C](#)) and lived in areas with tall bamboo culms ( $\beta = 0.56$ ,  $P < 0.001$ , [Figure 3I](#)), however, they appeared to be insensitive to human-walking tracks ( $\beta = -0.31$ ,  $P < 0.005$ , [Figure 3B](#)).



**Figure 2.** Visualization of habitat utilization of red pandas on annual scale. The utilization intensity increases from green to blue. Orange and gray lines represent roads and human-walking tracks while red dots show human habitat sites. Highly utilized areas were close to water sources having bamboo abundance.

The averaged model for the cub-rearing season included most of the covariates (Table 2). Collared animals moved to high elevations ( $\beta = 0.66$ ,  $P < 0.03$ , Figure 3J) and were attracted to the mountain ridges ( $\beta = 0.38$ ,  $P < 0.03$ , Figure 3M) in this season. Aspect appeared to be influential only for the cub-rearing season (Figure 3N and Supplementary Table S2). Red pandas showed affinity for south ( $\beta = 3.51$ ,  $P < 0.001$ ), southwest ( $\beta = 3.30$ ,  $P < 0.001$ ), west ( $\beta = 2.59$ ,  $P < 0.004$ ), and north ( $\beta = 2.37$ ,  $P < 0.02$ ) aspects. They selected areas that had high tree richness ( $\beta = 0.36$ ,  $P < 0.001$ , Figure 3F) with tall bamboo ( $\beta = 1.02$ ,  $P < 0.001$ , Figure 3I) and high shrub cover ( $\beta = 0.58$ ,  $P < 0.006$ , Figure 3H) in the understorey. However, they avoided large trees ( $\beta = -0.37$ ,  $P < 0.05$ , Figure 3E) and lived farther from roads ( $\beta = 0.5$ ,  $P < 0.005$ , Figure 3A) and human-walking tracks ( $\beta = 0.54$ ,  $P < 0.005$ , Figure 3B). They showed negative, but not significant, responses to the NDVI ( $\beta = -0.26$ ,  $P = 0.08$ , Figure 3D).

Red pandas exhibited inter-season variation in elevation use (Kruskal–Wallis rank-sum test = 347.9,  $df = 3$ ,  $P < 0.001$ ) and the post-hoc test (Dunn test) showed that they used higher elevation in the mating season than other seasons ( $P < 0.01$ , Supplementary Figure S2A).

The selected models revealed individual variation in habitat selection in pre-mating (marginal/conditional  $R^2$  0.13/0.69) and mating seasons (0.3/0.37), while such variation was negligible in the birthing (0.34/0.34) and cub-rearing seasons (0.37/0.37). The  $k$ -fold model validation showed good predictive performance of all seasonal models ( $r_s = 0.79$ – $0.96$ , Supplementary Table S3).

## Discussion

Our study provides the first fine-scale empirical evidence of the role of geo-physical, vegetation, and disturbance variables in seasonal

resource selection of red pandas. The combination of geo-physical, vegetation, and disturbance variables influenced resource selection although their effect varied across seasons. However, as a group, disturbance variables were influential in all seasons. While our data did not discriminate the role of geo-physical and vegetation variables, other unmeasured factors, such as forage availability, predation risk, disturbances, and thermoregulation appeared to have influenced their response to geo-physical variables. Red pandas appear to be highly selective in habitat selection while rearing their cubs as the selected model of this season included more variables than other seasons. Variables of all 3 groups (geo-physical, vegetation, and disturbance categories) equally contributed to the selected model of this season. These findings provide further support for the hypothesis that red panda's habitat selection changes seasonally in response to geo-physical attributes, vegetation-specific habitat features, and disturbances. We did not observe remarkable variation in habitat selection between males and females.

The influence of geo-physical variables appeared to be high in the cub-rearing and pre-mating seasons which may be explained by forage quality and risk avoidance behavior. Red pandas inhabited steeper slopes ( $>28^\circ$ ) in the pre-mating season. Living on steeper slopes provides better refuge from predators (Sarmiento and Berger 2020) which can help in minimizing the energetic cost of vigilance and escaping from predators and avoiding human encounters (Salandre et al. 2017). Red pandas preferred to stay in elevated areas with low human activities which could also have aided predator detection in the cub-rearing season (Crowell et al. 2016; Lowrey et al. 2017). Their movement across the elevation gradient was restricted within a narrow range of 817 m (2,468–3,285 m) throughout the year which corroborates a previous report from the adjoining Singalila National Park (Pradhan et al. 2001) and central Nepal

**Table 2** Candidate models describing habitat utilization as a function of geo-physical, vegetation, and disturbance variables for each season

Models	<i>df</i>	AICc	$\Delta$ AICc	Weight
<b>Premating season</b>				
Sola + Slop + Road_dist + Catt_dist + Elev	9	390.95	–	0.63
Sola + Slop + Road_dist + Catt_dist + Elev + Wat_dis	10	392.05	1.09	0.37
Tre_rich + Sola + Shu_cov + Bam_hei + Tre_dbh + NDVI + Elev + Trac_dist + Road_dist + Aspect + TPI + Wat_dis	22	837.90	4.53	0.06
<b>Mating season</b>				
Catt_dist + Trac_dist + Sex + Shu_cov + NDVI + Tre_cov	10	1,150.82	–	0.69
Catt_dist + Trac_dist + Sex + Shu_cov + NDVI + Tre_cov + Bam_cov	11	1,152.38	1.56	0.31
Catt_dist + Trac_dist + Sex + Shu_cov + NDVI + Tre_cov + Bam_cov + Road_dist	12	1,153.80	3.00	0.12
<b>Birthing season</b>				
Catt_dist + Bam_hei + Trac_dist + Tre_cov	8	903.79	–	0.33
Catt_dist + Bam_hei + Trac_dist + Tre_cov + NDVI	9	904.2	0.44	0.27
Catt_dist + Bam_hei + Trac_dist + Tre_cov + TPI + NDVI	10	904.9	1.07	0.19
Catt_dist + Bam_hei + Trac_dist + Tre_cov + TPI + NDVI + Elev	11	906.00	2.25	0.11
<b>Cub-rearing season</b>				
Tre_rich + Shu_cov + Bam_hei + NDVI + Tre_dbh + Trac_dist + TPI + Elev + Aspect + Road_dist	20	832.10	–	0.55
Tre_rich + Sola + Shu_cov + Bam_hei + NDVI + Tre_dbh + Trac_dist + TPI + Elev + Aspect + Road_dist	21	833.20	1.13	0.31
Tre_rich + Sola + Shu_cov + Bam_hei + Slop + NDVI + Tre_dbh + Trac_dist + TPI + Elev + Aspect + Road_dist	22	835.4	3.28	0.11

Model selection was based on averaged model from the set of top models with  $\Delta$ AICc < 2.

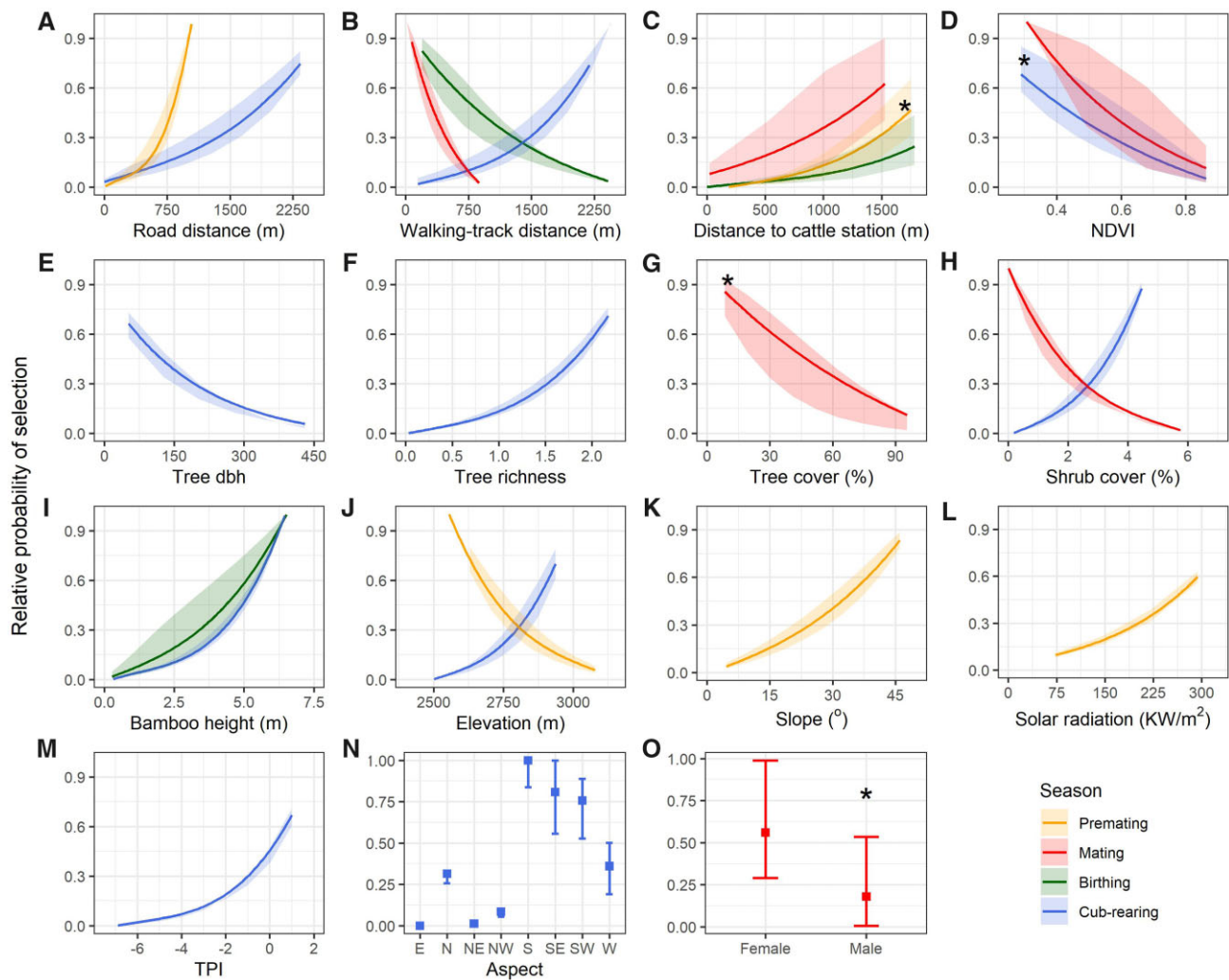
(Yonzon and Hunter 1991). Such a narrow range supports red panda's specialist nature and perhaps indicates potential vulnerability to climate change. Despite they occupied higher elevation in the mating season than other seasons, their within-season movement across the elevation gradient was more obvious in cub-rearing and pre-mating seasons. Furthermore, they covered wider range in the birthing and cub-rearing seasons. Such a variation could be attributed as their response to environmental conditions (Tablado et al. 2014), food quality (Smolko et al. 2018), human disturbances (Gill et al. 2001), and predation risk (Lendrum et al. 2018; Peers et al. 2020). However, these observations warrant further research using a larger sample size of red panda in habitat with a larger elevation gradient, preferably up to the tree line.

The selected model for the cub-rearing season included aspect even though red pandas mostly selected south, southwest, and west aspects throughout the year. This observation contradicts previous findings that red pandas use north, northeast, and northwest aspects (Yonzon et al. 1991; Bista et al. 2017; Shrestha et al. 2021). We attribute this contrast to underlying variation in micro-habitat in the different areas. We found that the selected aspect had linear relationship with solar insolation ( $r=0.38$ ,  $P=0.03$ ) and bamboo height ( $r=0.39$ ,  $P=0.02$ ) where bamboo cover was significantly higher (>16%) than the unselected ones ( $t=-4.3$ ,  $df=6$ ,  $P<0.002$ ). This indicates that the selection of aspect helps in securing food with minimal effort (Salandre et al. 2017) and aids in thermoregulation (Hull et al. 2016), which is consistent with the optimal foraging hypothesis. Surprisingly, none of our seasonal models included water as a significant predictor which contradicts with the previous reports (Yonzon and Hunter 1991; Pradhan et al. 2001; Dorji et al. 2011; Bista et al. 2017, 2019). This lack of influence may be due to regular snowfalls in the winter that provided water and ensured water availability throughout the year. However, we recorded 79.6% of the GPS fixes within 100 m of water across all seasons which is consistent with previous reports (Yonzon and Hunter 1991; Pradhan et al. 2001; Bista et al. 2017). This

observation suggests that free water is so ubiquitous in our study area that it did not show up as a significant explanatory variable, and it may remain that water is a crucial covariate in determining red panda habitat use.

The selected models of all seasons except the pre-mating season comprised vegetation variables but the micro-habitat of selected areas varied across these seasons. Selection of high shrub cover in the cub-rearing season can provide better concealment while feeding on bamboo shoots on the ground (Crowell et al. 2016) while tree rich areas can offer supplementary diets (Acharya et al. 2018). The climatic parameters of the study area further explain this variation. The red panda birthing season overlaps with the onset of the monsoon which stimulates bamboo growth and improves the habitat quality across most of their range. Animals living in high-quality habitat have the option of selecting the best habitat patches while they become less selective in a mixture of high and poor-quality habitat (Pyke 1984; William et al. 2018). For this reason, red pandas may have selected the best available patches with tall bamboo amidst rich environmental conditions in the birthing season. In contrast, low shrub cover, tree cover, and NDVI were associated with low temperatures and snowfall in the mating season. The study animals primarily inhabited broad-leaf mixed forest where most of the trees shed their leaves in winter which affected the tree cover and NDVI. Red pandas visited some of these deciduous trees, such as *Sorbus* spp. and *A. callosa* to supplement their diet. We assume that low winter nutritional value of bamboo and other diet species also contribute to the resource selection of red pandas. Further research needs to be carried out in order to validate this hypothesis.

Consistent with our a priori hypothesis, red pandas avoided disturbances throughout the year which corroborates previous reports (Yonzon et al. 1991; Acharya et al. 2018; Panthi et al. 2019). They avoided cattle stations in all seasons, except in the cub-rearing season. However, the median distance (1,399 m) to cattle stations was the farthest in this season than any other season ( $P<0.001$ ) although the selected model did not include this covariate. Red pandas



**Figure 3.** Predicted relative probability of selection of variables across seasons. Only the significant ( $P < 0.05$ ) and marginally significant variables (highlighted with asterisks,  $P > 0.05 < 0.09$ ) of the selected models of each season (Supplementary Table S2) are presented in this plot. In panels A–M, solid lines represent predicted probability of selection of the respective covariates while the colored ribbons connote 95% CI. In panel N, the square box and error bars represent the predicted probability of resource selection of aspects and 95% CI, respectively. Panel O shows the predicted probability of resource selection by males and females. Predicted and confidence intervals are scaled to have values ranging between 0 and 1.

also avoided roads in the pre-mating and cub-rearing seasons while the selected models for the other 2 seasons did not include this variable. While this is true, the median distance between the area used by red panda and roads was the farthest (554 m, IQR 217–1,378 m) in the birthing season. Surprisingly, red pandas were flexible in selecting and avoiding areas close to human-walking tracks across different seasons. The motive behind using habitat close to human-walking tracks, by red panda, in the mating season may be different than in the birthing season.

We observed males being less selective in habitat use in this season which suggests that the mating instinct drives males to find receptive females. Similarly, females live alone without any dependents in this season. Therefore, both males and females are likely to become less risk averse. In the birthing season in our study period, the low traffic along the human-walking tracks (0.06 individuals/day during a COVID-19 pandemic) perhaps means red pandas did not need to avoid these features (Bista et al. 2021a). Despite this contrasting response toward the walking tracks, females appeared to have lived farther from walking tracks in the birthing

season. Such a response is expected in females while they are with their dependents (Brown et al. 1999), and 3 females had dependent cubs in our study. Such a pattern demonstrates that red pandas perceive walking tracks as a risk albeit the degree of perceived risk varies across seasons. This may be due to differences in biological requirements which is further aggravated by traffic volume (Bista et al. 2021a). However, this observation warrants further study on the use of such features across the diel cycle.

Individual variation in resource selection was detected in only 2 seasons. High individual variation can be expected in poor-quality habitat when disturbances are high, as individual animals are likely to adopt different behavioral tactics to adapt in individual situations (Bonnot et al. 2015). It was evident in our study as among-individual variation was high in pre-mating and mating seasons when the habitat quality was relatively poor in comparison to the habitat status in birthing and cub-rearing seasons. However other factors, such as its age, sex, biological requirements, and the physiological state of an individual can also contribute to individual variation in behavior (Leclerc et al. 2016; Hertel et al. 2020). The



variation in energy requirements and perceived risk was high for mothers who were living with dependent cubs in the pre-mating season, while cubs dispersed and started to live independently in the mating season. The limited experience of dispersers and increased mating behaviors of adult males and females would have further contributed to high individual variation in the mating season. Despite the contrasting variation in habitat selection at an individual level this is, to some extent, evidence of red pandas' flexibility to adapt in heterogeneous habitat. Yet it may lead to local extirpation unless they succeed in doing so. Therefore, information on the fitness levels of animals living in such habitat would help establish more evidence on this matter.

Notwithstanding the relatively small sample size, this study demonstrates the importance of minimizing disturbances throughout the year and highlights the role of micro-habitat during their biologically crucial phases. We suggest restricting human activities, especially, during the mating and cub-rearing seasons and avoiding road construction within the core area. Findings further bolstered the need for livestock-herding management within the red panda range. However, the presence of contradictory patterns for some of the variables across seasons reinforces the challenges of making simple red panda-informed land management conservation decisions. What might be beneficial in 1 season, could be detrimental in another. Therefore, we suggest considering geo-physical, vegetation, and disturbance variables bearing in mind the background context of season while formulating conservation plans. Additionally, this study was limited within the home range scale which warrants further study on multi-scale approach to delve deeper into the understanding of resource selection patterns.

## Authors' Contributions

D.B., G.S.B., N.J.H., and P.J.M. conceived and designed the study. D.B. conducted field survey, performed data analysis, and wrote the manuscript. All authors reviewed and approved the work before submission.

## Acknowledgments

We acknowledge the support from the Divisional Forest Office, Ilam, Sandakpur Rural Municipality, The Mountain Organization, and Shree Deep Jyoti Youth Club. We are grateful to Ang Phuri Sherpa and Sonam Tashi Lama for their support in managing this project on the ground. We are also grateful to Janno Weerman for his help in securing resources for this study. We thank Ngima Dawa Sherpa, Gyajo Lama Bhoté, Wangchu Bhutia, Purushotam Pandey, Sita Gurung, Jiwan Rai, Surendra Rai, Aadesh Khamdak, Pema Bhutia, RPN's forest guardians, and local people who assisted during the field work. This study was approved by the University of Queensland's Animal Ethics Committee (SAFS/133/19/NEPAL), and the Department of Forests and Soil Conservation, Government of Nepal (DFSC-521/075/076 and DFSC-244/076/077).

## Funding

This study was funded by Rotterdam Zoo and Red Panda Network. D.B. was supported by the University of Queensland for a research training scholarship and Wildlife Conservation Network for the Handsel scholarship.

## Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

## Conflict of Interest Statement

We declare no potential conflicts of interest.

## References

- Acharya KP, Shrestha S, Paudel PK, Sherpa AP, Jnawali SR et al., 2018. Pervasive human disturbance on habitats of endangered red panda *Ailurus fulgens* in the central Himalaya. *Glob Ecol Conserv* 15:e00420.
- Allen RB, Forsyth DM, Allen RKJ, Affeld K, MacKenzie DI, 2015. Solar radiation determines site occupancy of coexisting tropical and temperate deer species introduced to New Zealand forests. *PLoS ONE* 10:e0128924.
- Bista D, Baxter GS, Hudson NJ, Lama ST, Murray PJ, 2021a. Effect of disturbances and habitat fragmentation on an arboreal habitat specialist mammal using GPS telemetry: A case of the red panda. *Lands Ecol*.
- Bista D, Baxter GS, Hudson NJ, Lama ST, Weerman J et al., 2021b. Movement and dispersal of a habitat specialist in human-dominated landscapes: A case study of the red panda. *Mov Ecol* 9:62.
- Bista D, Baxter GS, Hudson NJ, Lama ST, Weerman J et al., 2022a. Space use, interaction and recursion in a solitary specialized herbivore: A red panda case study. *End Species Res* 47:131–143.
- Bista D, Bhattarai B, Shrestha S, Lama ST, Dhamala MK et al., 2022b. Bamboo distribution in Nepal and its impact on red pandas. In: Glatston AR, editor. *Red Panda: Biology and Conservation of the First Panda*. Oxford: Academic Press. 353–368.
- Bista D, Lama ST, Weerman J, Sherpa AP, Pandey P et al., 2021c. Improved trapping and handling of an arboreal, montane mammal: Red panda *Ailurus fulgens*. *Animals* 11:921.
- Bista D, Paudel PK, Jnawali SR, Sherpa AP, Shrestha S et al., 2019. Red panda fine-scale habitat selection along a Central Himalayan longitudinal gradient. *Ecol Evol* 9:5260–5269.
- Bista D, Shrestha S, Sherpa P, Kokh M, Khanal K et al., 2017. Distribution and habitat use of red panda in the Chitwan-Annapurna Landscape of Nepal. *PLoS ONE* 12:e0178797.
- Blecha KA, Boone RB, Alldredge MW, Gaillard JM, 2018. Hunger mediates apex predator's risk avoidance response in wildland–urban interface. *J Anim Ecol* 87:609–622.
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR et al., 2009. Generalized linear mixed models: A practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135.
- Bonnot N, Verheyden H, Blanchard P, Cote J, Debeffe L et al., 2015. Interindividual variability in habitat use: Evidence for a risk management syndrome in roe deer? *Behav Ecol* 26:105–114.
- Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA, 2002. Evaluating resource selection functions. *Ecol Model* 157:281–300.
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW et al., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400.
- Brown JS, Laundré JW, Gurung M, 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. *J Mammal* 80:385–399.
- Burnham KP, Anderson DR, Huyvaert KP, 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behav Ecol Sociobiol* 65:23–35.
- Crooks KR, 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conserv Biol* 16:488–502.
- Crowell MM, Shipley LA, Camp MJ, Rachlow JL, Forbey JS et al., 2016. Selection of food patches by sympatric herbivores in response to concealment and distance from a refuge. *Ecol Evol* 6:865–2876.
- Dalui S, Khatri H, Singh SK, Basu S, Ghosh A et al., 2020. Fine-scale landscape genetics unveiling contemporary asymmetric movement of red panda *Ailurus fulgens* in Kangchenjunga landscape, India. *Sci Rep* 10:12.
- De Reu J, Bourgeois J, Bats M, Zwervaegher A, Gelorini V et al., 2013. Application of the topographic position index to heterogeneous landscapes. *Geomorphology* 186:39–49.
- DeGiudice GD, Sampson BA, Giudice JH, 2013. A long-term assessment of the effect of winter severity on the food habits of white-tailed deer. *J Wildl Manage* 77:1664–1675.

- Dendup P, Cheng E, Lham C, Tenzin U, 2017. Response of the endangered red panda *Ailurus fulgens fulgens* to anthropogenic disturbances, and its distribution in Phrumsengla National Park, Bhutan. *Oryx* 51:701–708.
- Dendup P, Humle T, Bista D, Penjor U, Lham C et al., 2020. Habitat requirements of the Himalayan red panda *Ailurus fulgens* and threat analysis in Jigme Dorji National Park, Bhutan. *Ecol Evol* 10:9444–9453.
- Dorji S, Vernes K, Rajaratnam R, 2011. Habitat correlates of the red panda in the temperate forests of Bhutan. *PLoS ONE* 6:e26483.
- Edomwande C, Barbosa F, 2020. The influence of predation risk on mate signaling and mate choice in the lesser waxmoth *Achroia grisella*. *Sci Rep* 10: 524.
- Eldegard K, Lyngved JT, Hjeljord O, 2012. Coping in a human-dominated landscape: Trade-off between foraging and keeping away from roads by moose *Alces alces*. *Eur J Wildl Res* 58:969–979.
- ESRI, 2020. *ArcMap 10.8*. Redlands (CA): Environmental Systems Research Institute.
- Fleming CH, Clalabrese JM, 2021. *ctmm: Continuous-Time Movement Modeling*. R package version 0.6.0. Available from: <https://CRAN.R-project.org/package=ctmm>.
- Fox J, Monette G, 1992. Generalized collinearity diagnostics. *J Am Stat Assoc* 87:178–183.
- Fox J, Yonzon P, Podger N, 1996. Mapping conflicts between biodiversity and human needs in Langtang National Park, Nepal. *Conserv Biol* 10:562–569.
- Gill JA, Norris K, Sutherland WJ, 2001. Why behavioural responses may not reflect the population consequences of human disturbance. *Biol Conserv* 97: 265–268.
- Glatston A, Wei F, Zaw T, Sherpa A, 2015. *Ailurus fulgens*. The IUCN Red List of Threatened Species 2015: e.T714A110023718. Available from: <https://www.iucnredlist.org/species/714/110023718> (accessed 5 October 2020).
- Graham MD, Douglas-Hamilton I, Adams WM, Lee PC, 2009. The movement of African elephants in a human-dominated land-use mosaic. *Anim Conserv* 12:445–455.
- Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A et al., 2015. Habitat fragmentation and its lasting impact on Earth's. *Ecosyst Sci Adv* 1: e1500052.
- Hansen MC, Riggs RA, 2008. Accuracy, precision, and observation rates of Global Positioning System telemetry collars. *J Wildl Manage* 72:518–526.
- Harrison XA, 2015. A comparison of observation-level random effect and beta-binomial models for modelling overdispersion in binomial data in ecology and evolution. *PeerJ* 3:e1114.
- Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN et al., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6:e4794.
- Hebblewhite M, Merrill E, 2007. Modelling wildlife–human relationships for social species with mixed-effects resource selection models. *J Appl Ecol* 45: 834–844.
- Hebblewhite M, Percy M, Merrill EH, 2007. Are all global positioning system collars created equal? Correcting habitat-induced bias using three brands in the Central Canadian Rockies. *J Wildl Manage* 71:2026–2033.
- Hertel AG, Niemelä PT, Dingemans NJ, Mueller T, 2020. A guide for studying among-individual behavioral variation from movement data in the wild. *Mov Ecol* 8:30.
- Hu Y, Thapa A, Fan H, Ma T, Wu Q et al., 2020. Genomic evidence for two phylogenetic species and long-term population bottlenecks in red pandas. *Sci Adv* 6:eaax5751.
- Hull V, Zhang J, Huang J, Zhou S, Vina A et al., 2016. Habitat use and selection by giant pandas. *PLoS ONE* 11:e0162266.
- Johnson DH, 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Koper N, Manseau M, 2012. A guide to developing resource selection functions from telemetry data using generalized estimating equations and generalized linear mixed models. *Rangifer* 32:195.
- Krausman PR, 1999. Some basic principles of habitat use. In: Launchbaugh KL, Sanders KD, Mosley JL, editors. *Grazing Behavior of Livestock and Wildlife, Idaho Forest*. Moscow: University of Idaho. 85–90.
- Leclerc M, Vander Wal E, Zedrosser A, Swenson JE, Kindberg J et al., 2016. Quantifying consistent individual differences in habitat selection. *Oecologia* 180:697–705.
- Lendrum PE, Northrup JM, Anderson CR, Liston GE, Aldridge CL et al., 2018. Predation risk across a dynamic landscape: Effects of anthropogenic land use, natural landscape features, and prey distribution. *Lands Ecol* 33: 157–170.
- Lewis JS, Rachlow JL, Garton EO, Vierling LA, 2007. Effects of habitat on GPS collar performance: Using data screening to reduce location error. *J Appl Ecol* 44:663–671.
- Lowrey B, Garrott RA, Miyasaki HM, Fralick G, Dewey SR, 2017. Seasonal resource selection by introduced mountain goats in the southwest Greater Yellowstone Area. *Ecosphere* 8:e01769.
- Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP et al., 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Netherlands: Springer.
- Martin J, Basille M, Moorter BMV, Kindberg J, Allainé D et al., 2010. Coping with human disturbance: Spatial and temporal tactics of the brown bear *Ursus arctos*. *Can J Zool* 88:875–883.
- Menhinick EF, 1964. A comparison of some species-individuals diversity indices applied to samples of field insects. *Ecology* 45:859–861.
- Michel ES, Jenks JA, Kaskie KD, Klaver RW, Jensen WF, 2018. Weather and landscape factors affect white-tailed deer neonate survival at ecologically important life stages in the Northern Great Plains. *PLoS ONE* 13: e0195247.
- Nakagawa S, Schielzeth H, 2013. A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods Ecol Evol* 4: 133–142.
- Panthi S, Wang T, Sun Y, Thapa A, 2019. An assessment of human impacts on endangered red pandas living in the Himalaya. *Ecol Evol* 9:13413–13425.
- Pedersen SH, Bentzen TW, Reinking AK, Liston GE, Elder K et al., 2021. Quantifying effects of snow depth on caribou winter range selection and movement in Arctic Alaska. *Mov Ecol* 9:48.
- Peers MJL, Majchrzak YN, Menzies AK, Studd EK, Bastille-Rousseau G et al., 2020. Climate change increases predation risk for a keystone species of the boreal forest. *Nat Clim Change* 10:1149–1153.
- Pfeifer M, Lefebvre V, Peres C, Banks-Leite C, Wearn O et al., 2017. Creation of forest edges has a global impact on forest vertebrates. *Nature* 551: 187–191.
- Pradhan S, Saha GK, Khan JA, 2001. Ecology of the red panda *Ailurus fulgens* in the Singhalila National Park, Darjeeling, India. *Biol Conserv* 98:11–18.
- Pyke G, 1984. Optimal foraging theory: A critical review. *Annu Rev Ecol Syst* 15:523–575.
- Qi D, Hu Y, Gu X, Li M, Wei F, 2009. Ecological niche modeling of the sympatric giant and red pandas on a mountain-range scale. *Biodivers Conserv* 18:2127–2141.
- Reid DG, Hu J, Yan H, 1991. Ecology of the red panda *Ailurus fulgens* in the Wolong Reserve, China. *J Zool* 225: 347–364.
- Robert GDE, Robert S, Graham S, Christopher OK, 2002. GPS radiotelemetry error and bias in mountainous terrain. *Wildl Soc Bul* 30:430–439.
- Roberts DR, Bahn V, Ciuti S, Boyce MS, Elith J et al., 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography* 40:913–929.
- Rosenzweig ML, 1981. A theory of habitat selection. *Ecology* 62:327–335.
- Salandre JA, Beil R, Loehr JA, Sundell J, 2017. Foraging decisions of North American beaver *Castor canadensis* are shaped by energy constraints and predation risk. *Mammal Res* 62:229–239.
- Sarmento W, Berger J, 2020. Conservation implications of using an imitation carnivore to assess rarely used refuges as critical habitat features in an alpine ungulate. *PeerJ* 8:e9296.
- Sergio F, Marchesi L, Pedrini P, Penteriani V, 2007. Coexistence of a generalist owl with its intraguild predator: Distance-sensitive or habitat-mediated avoidance? *Anim Behav* 74:1607–1616.
- Seto T, Matsuda N, Okahisa Y, Kaji K, 2015. Effects of population density and snow depth on the winter diet composition of sika deer. *J Wildl Manage* 79:243–253.

- Sharma HP, Belant JL, Swenson JE, 2014. Effects of livestock on occurrence of the Vulnerable red panda *Ailurus fulgens* in Rara National Park, Nepal. *Oryx* 48:228–231.
- Sheppard AHC, Hecker LJ, Edwards MA, Nielsen SE, 2021. Determining the influence of snow and temperature on the movement rates of wood bison *Bison bison athabasca*. *Can J Zool* 99:489–496.
- Shrestha S, Thapa A, Bista D, Robinson N, Sherpa AP et al., 2021. Distribution and habitat attributes associated with the Himalayan red panda in the westernmost distribution range. *Ecol Evol* 11: 4023–4034.
- Smolko P, Veselovská A, Kropil R, 2018. Seasonal dynamics of forage for red deer in temperate forests: Importance of the habitat properties, stand development stage and overstorey dynamics. *Wildl Biol* 2018:1–10.
- Subba S, Ma Y, Ma W, 2019. Spatial and temporal analysis of precipitation extremes of eastern Nepal in the last two decades (1997–2016). *J Geophys Res Atmos* 124:7523–7539.
- Tablado Z, Fauchald P, Mabilille G, Stien A, Tveraa T, 2014. Environmental variation as a driver of predator–prey interactions. *Ecosphere* 5:art164–13.
- Thapa A, Wu R, Hu Y, Nie Y, Singh PB et al., 2018. Predicting the potential distribution of the endangered red panda across its entire range using MaxEnt modeling. *Ecol Evol* 8:10542–10554.
- Thapa K, Thapa GJ, Bista D, Jnawali SR, Acharya KP et al., 2020. Landscape variables affecting the Himalayan red panda *Ailurus fulgens* occupancy in wet season along the mountains in Nepal. *PLoS ONE* 15:e0243450.
- Tucker MA, Böhning-Gaese K, Fagan WF, Fryxell JM, Van Moorter B et al., 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* 359:466–469.
- Tucker MA, Santini L, Carbone C, Mueller T, 2021. Mammal population densities at a global scale are higher in human-modified areas. *Ecography* 44:1–13.
- Wei F, Feng Z, Wang Z, Hu J, 2000. Habitat use and separation between the giant panda and the red panda. *J Mammal* 81:448–455.
- Wevers J, Fattebert J, Casaer J, Artois T, Beenaerts N, 2020. Trading fear for food in the Anthropocene: How ungulates cope with human disturbance in a multi-use, suburban ecosystem. *Sci Tot Environ* 741:140369.
- William G, Jean-Michel G, Sonia S, Christophe B, Atle M et al., 2018. Same habitat types but different use: Evidence of context-dependent habitat selection in roe deer across populations. *Sci Rep* 8:5102.
- Williams BH, 2006. Red panda in eastern Nepal: How do they fit into eco-region conservation of the eastern Himalaya. In: McNeely JA, McCarthy TM, Smith A, Olsvig-Whittaker L, Wikramanayake ED, editors. *Conservation Biology in Asia*. Kathmandu (Nepal): The Society for Conservation Biology Asia Section and Resources Himalaya. 236–251.
- Williams CM, Ragland GJ, Betini G, Buckley LB, Cheviron ZA et al., 2017. Understanding evolutionary impacts of seasonality: An introduction to the symposium. *Integr Comp Biol* 57:921–933.
- Yonzon P, 1989. Ecology and conservation of the red panda in the Nepal Himalayas [The graduate school PhD thesis]. [Orono (ME)]: University of Maine.
- Yonzon P, Jones R, Fox J, 1991. Geographic information systems for assessing habitat and estimating population of red pandas in Langtang National Park, Nepal. *AMBIO* 20:285–285.
- Yonzon PB, Hunter ML, 1991. Conservation of the red panda *Ailurus fulgens*. *Biol Conserv* 57:1–11.
- Zhang M, Zhang Z, Li Z, Hong M, Zhou X et al., 2018. Giant panda foraging and movement patterns in response to bamboo shoot growth. *Environ Sci Pollut Res* 25:8636–8643.
- Zhang Z, Hu J, Yang J, Li M, Wei F, 2009. Food habits and space-use of red pandas *Ailurus fulgens* in the Fengtongzhai Nature Reserve, China: Food effects and behavioural responses. *Acta Theriol* 54:225–234.
- Zhang Z, Wei F, Li M, Zhang B, Liu X et al., 2004. Microhabitat separation during winter among sympatric giant pandas, red pandas, and tufted deer: The effects of diet, body size, and energy metabolism. *Can J Zool* 82: 1451–1458.