



Effect of disturbances and habitat fragmentation on an arboreal habitat specialist mammal using GPS telemetry: a case of the red panda

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Abstract

Context Habitat specialists residing in human-modified landscapes are likely to be more vulnerable to disturbance because of a functional reliance on very particular habitat features. However, there have been few studies designed to specifically address that issue.

Objectives This study aimed to explore how the red panda, an iconic endangered habitat specialist, behaves when faced with disturbances and habitat fragmentation. In particular, we attempted to examine the effect of anthropogenic disturbances and fragmentation on home-range size, activity patterns, and recursion.

Methods Using GPS telemetry we monitored 10 red pandas and documented disturbances using camera trapping for one year in eastern Nepal. We performed

spatial analysis, analysed activity patterns and evaluated the effect of habitat fragmentation and disturbances on home-range size and residence time using Linear Mixed Models.

Results Home-range size increased in areas with low availability of forest cover whilst home ranges were smaller in areas with a high road density. Red pandas spent more time in large habitat patches away from roads and cattle stations. Crossing rates suggested that roads acted as a barrier for movement across their habitat. Red pandas also partitioned their activity to minimize interactions with disturbances.

Conclusions Red pandas seem to make a trade-off to co-exist in human-dominated landscapes which may have adverse long-term effects on their survival. This indicates that current patterns of habitat fragmentation and forest exploitation may be adversely affecting red panda conservation efforts and that landscape-scale effects should be considered when planning conservation actions.

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Keywords Home range · Habitat fragmentation · Barrier effect · Activity pattern · Residence time · Anthropogenic disturbances

Introduction

Human activities are increasingly modifying forests making them less suitable for wild animals (Haddad

et al. 2015). Habitat fragmentation is the most obvious effect influencing the survival of forest inhabitants by converting the landscape into a mosaic of suitable habitat within a matrix of habitat that has been altered to some degree (Fahrig 2003; Fletcher et al. 2018). Animals living in such a landscape may have to compromise with limited food, resting, hiding and nesting resources, even to the point the species living in such habitat may become less resilient during natural disasters (Malhi et al. 2008; Schwitzer et al. 2011). Predator pressure is also higher in degraded habitat (Schneider 2001), and wildlife perceive such areas as more risky (Mendes et al. 2020). Nonetheless, wildlife must compromise between occupying such degraded habitat and avoiding predation risk and/or human-induced disturbances (Gill et al. 2001) where living in the degraded habitat is always associated with increased risk of mortality (Frid and Dill 2002). But the response towards disturbances and habitat fragmentation varies across species (Haddad et al. 2015; Tucker et al. 2018). Wildlife managers should know how a particular species responds to such threats so that they can devise and prioritize conservation measures to fit the target species in specific habitats.

Disturbances may obstruct movement or limit access to suitable habitat and thereby result in habitat avoidance, limited habitat use, reduced time spent on feeding and physiological changes (Frid and Dill 2002). Roads may hinder migration and dispersal, impede animal movement, reduce connectivity and constrain species interactions (Forman and Alexander, 1998; Angelsen and Kaimowitz 1999). Many species purposefully avoid fragmented habitat, human presence and disturbances (Haddad et al. 2015). For instance some animals occupy less or more space in human-dominated landscapes (Martin et al. 2010; Jerina 2012), avoid low-quality patches and occupy better habitat (Martin et al. 2010), stay away from areas close to disturbance sources (Hebblewhite and Merrill 2008; Graham et al. 2009), and adapt to be less active when human activity is greatest (Hebblewhite and Merrill 2008; De Oliveira et al. 2014; Wevers et al. 2020).

Adaptation to disturbances is an attribute to survive in human-dominated landscapes (Johann et al. 2020). Wild animals have the capacity to tolerate disturbances to certain levels (Lowrey and Longshore 2017; New et al. 2020), but animals with low plasticity are under high risk of extirpation and extinction (Ciuti

et al. 2012a). Prolonged exposure to disturbances may habituate some animals (Higham and Shelton 2011; Geffroy et al. 2015), and makes them more susceptible to poaching (Bejder et al. 2009) and predation risk (Geffroy et al. 2015). Furthermore, the magnitude of effects vary over time resulting in long-term cumulative effects (Berthinussen and Altringham 2012), and affect individual's fitness and lead to reduced survival and reproductive success at a population level (Frid and Dill 2002).

GPS telemetry has been rarely used in studying the effect of disturbances and habitat fragmentation on arboreal mammals (Rus et al. 2020). Most of the available studies on responses of arboreal mammals to habitat fragmentation and disturbances are based on sign surveys, e.g. marsupials (Youngentob et al. 2013; Lindenmayer et al. 2021), primates (Almeida-Rocha et al. 2017; Kaisin et al. 2021) and tropical mammals (Whitworth et al. 2019). Further, GPS telemetry coupled with camera trapping has not yet been applied in studying how arboreal mammals are adapting in human-dominated landscapes. Arboreal mammals are more susceptible to fragmentation and disturbances than any other mammalian community (Whitworth et al. 2019), but studying their ecology is difficult due to their special habitat use (Moore et al. 2021). For that reason, use of cutting-edge technology could provide more authentic evidence to improve our understanding on how arboreal mammals are coping with disturbances. We therefore aimed to study the effects of disturbances using GPS telemetry and camera trapping on an arboreal mammal, the red panda *Ailurus fulgens*.

The red panda is an endangered species inhabiting the temperate forests in the eastern Himalaya (Glatston et al. 2015; Hu et al. 2020). This medium-sized species is a diet specialist feeding almost exclusively on bamboo (Pradhan et al. 2001). Being a solitary, cryptic and territorial arboreal mammal, it is difficult to study in the wild (Yonzon 1989; Bista et al. 2021b). Habitat loss and fragmentation are the major threats to red panda conservation (Acharya et al. 2018; Dalui et al. 2020; Hu et al. 2020). Increasing pressure on red panda habitat due to roads, livestock herding and over-extraction of forest resources are likely to threaten red panda survival (Fox et al. 1996; Acharya et al. 2018; Panthi et al. 2019). Similarly, herders' dogs can present a direct threat to red pandas (Yonzon and Hunter 1991). There have been examples of abandonment of habitat and local extirpation of red pandas in

some areas in China (Zhang et al. 2017) and Nepal (Bista et al. 2017). These reports suggest the need of robust quantitative and systematic analysis of the ecological effects disturbances and habitat fragmentation on this threatened species.

The general objective of this study was to evaluate the effects of disturbances on space use and interaction patterns of red panda. We hypothesized that reduction in suitable habitat patches would lead to an increase in home range size in disturbed and fragmented habitats (Van Beest et al. 2011; Wall et al. 2021). Second, that roads and human tracks would act as a barrier of movement because such features have reduced cover (He et al. 2019), possess high predation risk (Bennet 1991), and threat from people and dogs (Frid and Dill 2002). Further, the possibility of roadkill due to collision with vehicles is high along roads (Grilo et al. 2012; De Oliveira et al. 2014). We also hypothesized that red pandas would partition their activity patterns and stay away from disturbances to avoid risk as the cost of living in proximity to disturbances is high (Hebblewhite and Merrill 2008; Wu et al. 2018; Wevers et al. 2020).

Methods

Data collection

We conducted this study in eastern Nepal which borders to India in the east (27.10244N, 87.98157E, Fig. 1). The elevation of the study area ranged between 1500 and 3636 m with a sub-tropical to temperate climate with a mean temperature of 13.1 ± 6.78 °C. Human settlements, roads, walking trails, and livestock herding activities were present throughout the year. This makes it an ideal site for studying the effect of disturbances and habitat fragmentation on red panda. There were more than 15 human-habitation sites with a population of nearly 700 people living in the vicinity of the study area (CBS 2012). We visited each cattle station and recorded their GPS locations. We captured and equipped 10 red pandas including six females and four males with GPS collars (LiteTrack Iridium 150 TRD) following a standard operating procedure (Bista et al. 2021b). Of

these, we collared seven individuals in site 1, and rest of the three animals in site 2 (Table 1). These sub-adults were 6–7 months old when collared. Both sites have been highly altered by human activities, but site 1 had higher density of road (5.7 vs 0.2 km/km²) and walking tracks than in site 2 (6.5 vs 1.4 km/km²) while site 2 was experiencing more herding activities than in site 1.

The GPS collars were set to record one fix every two hours. In the montane habitat, telemetry error can be high due to terrain obstruction and high canopy (Lewis et al. 2007). To minimize this error, we excluded GPS fixes with ≤ 2 satellites and omitted imprecise locations with the dilution of precision > 5 (Lewis et al. 2007; Bjørneraas et al. 2010). Further, we retained locations only within the elevation range of our study site between 1500 and 3606 m.

To document disturbance volume, human activity patterns, cattle movement, dog presence and vehicles we deployed 34 passive infrared motion detection trail cameras with LED no-glow flash (Bushnell 24MP Trophy Cam HD No-Glow, Bushnell 20MP Trophy Cam HD No-Glow) from 22 November 2019 through 25 November 2020. We placed cameras randomly along the human-walking tracks, roads and forest areas within known red panda home ranges. Each camera was fastened to a tree trunk at 40 cm above ground. We considered image captures of an individual separated by ≥ 30 min as an independent event. We recorded 55,506 independent images including red pandas in only eight independent events in six trail cameras. Such a small sampling size was insufficient to draw any inference, but telemetry-based data can also be used in temporal interaction studies (Meredith and Ridout 2014; Lashley et al. 2018; Edwards et al. 2021). So we considered telemetry data falling within a 45 m radius of each camera, including 25 m telemetry error and 20 m detection range, as an independent event of a red panda visiting camera locations which resulted in an additional 77 independent events. This distance threshold was based on our camera's detection range (~ 25 m), but the camera's detection range reduces by one fourth during dark hours (Rowcliffe et al. 2011). So, we reduced the range to 20 m.

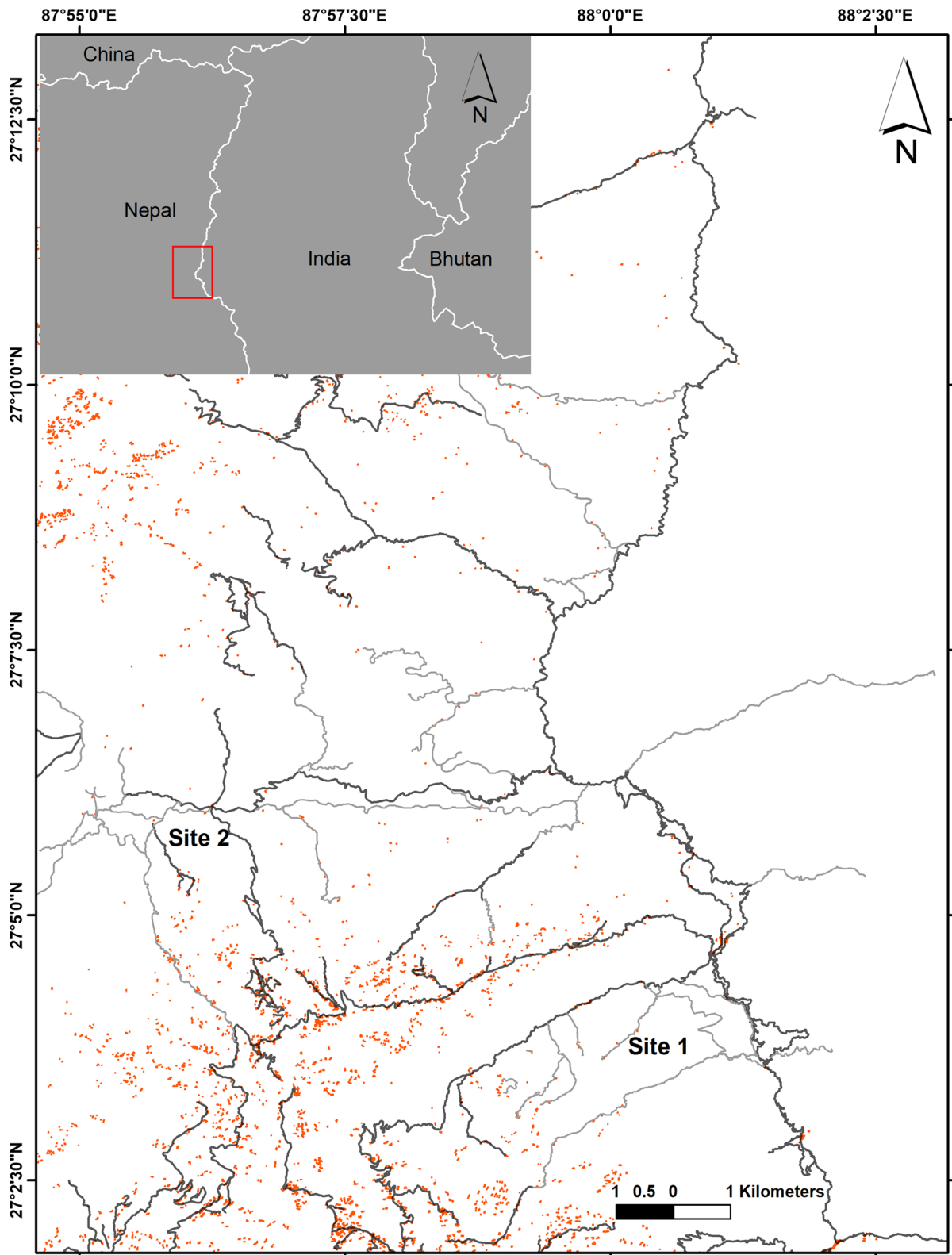


Fig. 1 Location of the study area. We carried out the study in Ilam and Panchthar districts, eastern Nepal which border India in the east. The inset shows the landscape features of the study area. Black and grey lines connote linear features: road and walking trails respectively. Human habitations are highlighted with orange dots. We captured and collared 10 red pandas in two sites: seven animals in Site 1 and three animals in Site 2

Table 1 Animals included in the study

Animals	Site 1	Site 2
Adult ♂	2	1
Adult ♀	3	1
Sub-adult ♂	1	
Subadult ♀	1	1

We collared seven individuals (two adult males, one sub-adult male, three adult female, one sub-adult female) in site 1, and three animals (one adult male, one adult female, one sub-adult female) in site 2

Data analyses

Effect of disturbance and fragmentation on space use

Initially we estimated home range size using weighted Autocorrelated Kernel Density estimation with 95% isopleth in the *ctmm* package (Calabrese et al. 2016). We accessed three Sentinel-2A satellite images of the study area taken between 15 October 2019 and 13 January 2020 at 10 m spatial resolution. Then we processed and analysed these images and classified land cover into forest and non-forest areas using the supervised classification method in ArcGIS following Sekertekin et al. (2017). This method of land use and land cover processing is commonly applied elsewhere for sentinel images (Phiri et al. 2020). Then we extracted the land cover area with annual and seasonal home ranges of each animal.

Patch level information barely provides clues for habitat fragmentation effects (Fahrig 2017). We therefore considered patch as well as class level metrics within home range. Patch area (AREA) and proportion of land cover availability (PLAND) were used to quantify the habitat configuration and land cover type in each animal's home range. We classified the land cover type into forest and non-forest areas. Our study area was in human-dominated landscape with roads, walking trails, cattle stations and human

habitation areas. Therefore, we used Connectance index (CONNECT), Clumpiness index (CLUMPY), Euclidean Nearest Neighbour Distance (ENN) and Patch Density (PD) metrics to measure the patch aggregation (Neel et al. 2004). The CONNECT refers to the proportion of functional joining of same class patches while the CLUMPY measures the degree to which patches are spatially aggregated (McGarigal 2015). We considered an average step length of red pandas (60 m) as a threshold distance to consider connectivity between neighbouring patches. The ENN measures the shortest straight-line distance between two same class patches. Likewise, PD facilitates the comparison of home ranges on severity of fragmentation level (McGarigal 2015). We also estimated road and human-walking track density within each animal's home range at annual and seasonal scales. We accessed these road and trail data from Open Street Map and visited the study sites to verify and improve the missing data. We performed the spatial analysis in Fragstat v4.2.1 (McGarigal et al. 2012) and ArcMap 10.8 (ESRI 2020).

We investigated recursion by computing residence time (total time spent in a location) and revisit (total number of visits to a previously visited location) using *recurse* package (Bracis et al. 2018). We considered average step length as a radius of an area (60 m), and 2 h as the time threshold to account for an independent visit between two successive visits.

Initially we examined the data for multicollinearity and omitted variables with the variation of inflation factor greater than 5 (Zuur et al. 2010). Then we evaluated the effect of habitat fragmentation and road density on home range size using a Linear Mixed Model (LMM) in *lme4* package (Bates et al. 2005). We included fragmentation metrics and road density as fixed factors. Using the LMM we also examined the effect of disturbances on residence time with distance to disturbance sources and fragmentation metrics as fixed factors. We included individual animals with a random intercept in the LMM. Then we run the model with all possible combinations and selected the candidate model based on the least corrected Akaike's Information Criterion (AICc) value (Burnham and Anderson 2002) using *MuMIn* package (Barton 2020). All these analyses were carried out in R (R Core Team 2020). We reported the marginal and conditional R^2 values to show the variation represented by the fixed and random effects (Nakagawa and Schielzeth 2013).

Barrier effect

For each red panda we investigated the barrier effect of roads and tracks. To do this we created each animal's movement trajectories between their successive GPS coordinates. Then we estimated crossing frequencies of these trajectories across roads and tracks in ArcMap. We categorised the crossing time into four unequal time categories: dawn, day, dusk and night following (Thieurmél and Elmarhraoui 2019).

We adopted one-way ANOVA to examine the mean difference in road and track densities and crossing rates for the animals with road and track presence in their home ranges. But we used a Kruskal–Wallis chi-squared test if the data was non-parametric. When examining whether these linear features affected animal movements we excluded data from animals that did not have those features in their home ranges ($n = 2$ for roads; $n = 2$ for pedestrian tracks). Using two-sample t-tests (hereafter t-test, for parametric data) and Wilcoxon rank-sum tests (for non-parametric data) we examined the differences between males and females. Due to insufficient location records we excluded one sub-adult from this analysis. We examined the difference in hourly road and track crossing rates for the animals with road and track presence in their home ranges using the Kruskal–Wallis test. We performed post-hoc analyses using Dunn tests to examine pair-wise differences (Dunn 1964). We also estimated the Spearman's correlation between road density and road crossing, and track density and track crossing.

Temporal interaction with disturbances

We sorted the camera images using Camera base 1.7 (Tobler 2007), and analysed the data in overlap (Ridout and Linkie 2009) and activity (Rowcliffe 2019) packages. We estimated the coefficient of overlap (Δ) to examine whether red pandas shifted their activity pattern to avoid disturbances due to dogs, vehicles, livestock and humans. We converted time into radians and selected 1 as smoothing parameter (Meredith and Ridout 2014). This overlap coefficient measures the degree of similarity between two kernel density distributions which ranges between 0 (no overlap) and 1 (complete overlap) (Ridout and Linkie 2009). We further tested difference in overall activity level of red pandas with disturbance sources using the

Wald test statistic (W) with 1 degree of freedom (Rowcliffe et al. 2014). We examined temporal interactions on annual and seasonal scales. We also tested the activity patterns along the human pedestrian tracks and forest areas.

Results

Effects of disturbances on space use

Home range and core area were positively correlated ($r = 0.96$, $p < 0.001$) so we considered only the home range to analyse the effect of fragmentation. The best-fit model comprised PLAND and road density as the influential predictors (Marginal $R^2 = 0.42$, Conditional $R^2 = 0.76$, Table S1). These predictors affected home range size negatively, but PLAND ($\beta = -0.22$, $SE = 0.05$, $p < 0.001$, Fig. 2a) had a stronger effect than road density ($\beta = -0.08$, $SE = 0.03$, $p < 0.001$, Fig. 2b).

The best-fit model for the residence time included four predictors (Marginal $R^2 = 0.08$, Conditional $R^2 = 0.23$, Table 2). The residence time increased in large habitat patches ($\beta = 269.98$, $p < 0.001$, Fig. 3a), away from roads ($\beta = 247.13$, $p < 0.001$, Fig. 3b) and cattle stations ($\beta = 120.41$, $p < 0.001$, Fig. 3c). It was high in areas close to human-walking tracks ($\beta = -75.73$, $p < 0.001$, Fig. 3d). The residence time and revisitations were positively correlated ($r = 0.78$, $p < 0.0001$). So, the above trends also apply for the number of revisits.

Barrier effect

The mean daily traffic volume on roads was 8.3 individual/day (4.4 vehicles, 3.1 people, 0.7 livestock, and 0.1 dog) while that on walking trails was 2.7 individuals/day (2.3 people, 0.4 livestock, and 0.05 dog). The mean road and track densities within the home range of each animal was $3.84 \pm 3.7/\text{km}^2$ (range 0–10) and 4.16 ± 4 (range 0–13) respectively. There was no significant variation between these densities ($F_{1,8} = 2.86$, $p = 0.129$, one-way ANOVA) in different home ranges where those features occurred. Neither was there a significant difference between red panda sexes and road ($t_8 = -1.03$, $p = 0.33$, t-test) and track densities ($t_8 = 0.22$, $p = 0.8$, t-test) within the home ranges. Red pandas

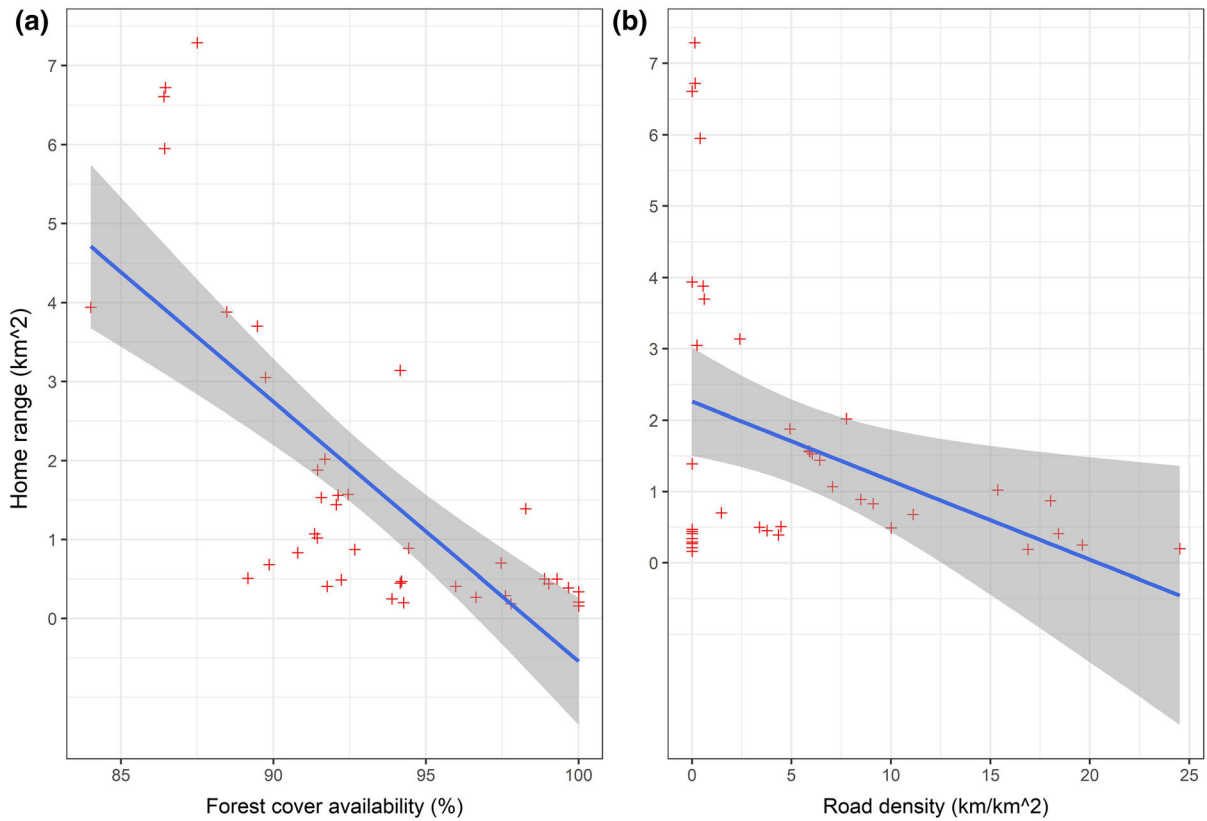


Fig. 2 The available forest cover (PLAND) and road density affected home range size. The blue line represents the trend line with grey ribbon as 95% CI while red cross denotes each data

point. **a** The home range increased with decrease in forest cover availability. **b** The home range decreased with increase in road density

Table 2 Candidate models describing residence time as a function of fragmentation indices and distance to disturbance sources

Models*	df	logLik	AICc	delta	Weight
AREA + Catt_dist + Road_dist + Trac_dist	7	− 36,591	73,196	0	1
Catt_dist + Road_dist + Trac_dist	6	− 36,600.6	73,213.1	17.1	0
AREA + Catt_dist + Road_dist	6	− 36,604.8	73,221.7	25.6	0
Catt_dist + Road_dist	5	− 36,614.3	73,238.7	42.7	0
AREA + Catt_dist + Trac_dist	6	− 36,667.9	73,347.7	151.7	0

*AREA Patch area, Catt_dist Distance to cattle station, Road_dist Distance to road, Trac_dist Distance to walking track

crossed roads and tracks 121 and 412 times respectively, and the crossing rate was significantly higher across tracks (median = 10, $X^2_{15} = 31.23$, $p = 0.008$, Kruskal–Wallis test).

The crossing rates varied across the diel cycle in roads ($X^2_{13} = 13.4$, $p < 0.004$, Kruskal–Wallis test) and tracks ($X^2_3 = 16.07$, $p < 0.002$, Kruskal–Wallis test, Fig. 4). The post-hoc test showed a significantly

higher road crossing rate during the day than in dawn ($z = -2.7$, $p = 0.03$) and dusk ($z = -3.22$, $p < 0.008$). Similarly, the track crossing rate by red panda was significantly higher in the day than at dawn ($z = -2.95$, $p < 0.02$) and dusk ($z = -2.93$, $p < 0.02$). We also observed the track crossing rate significantly higher in the night than at dawn ($z = -2.72$, $p < 0.03$) and dusk ($z = -2.7$,

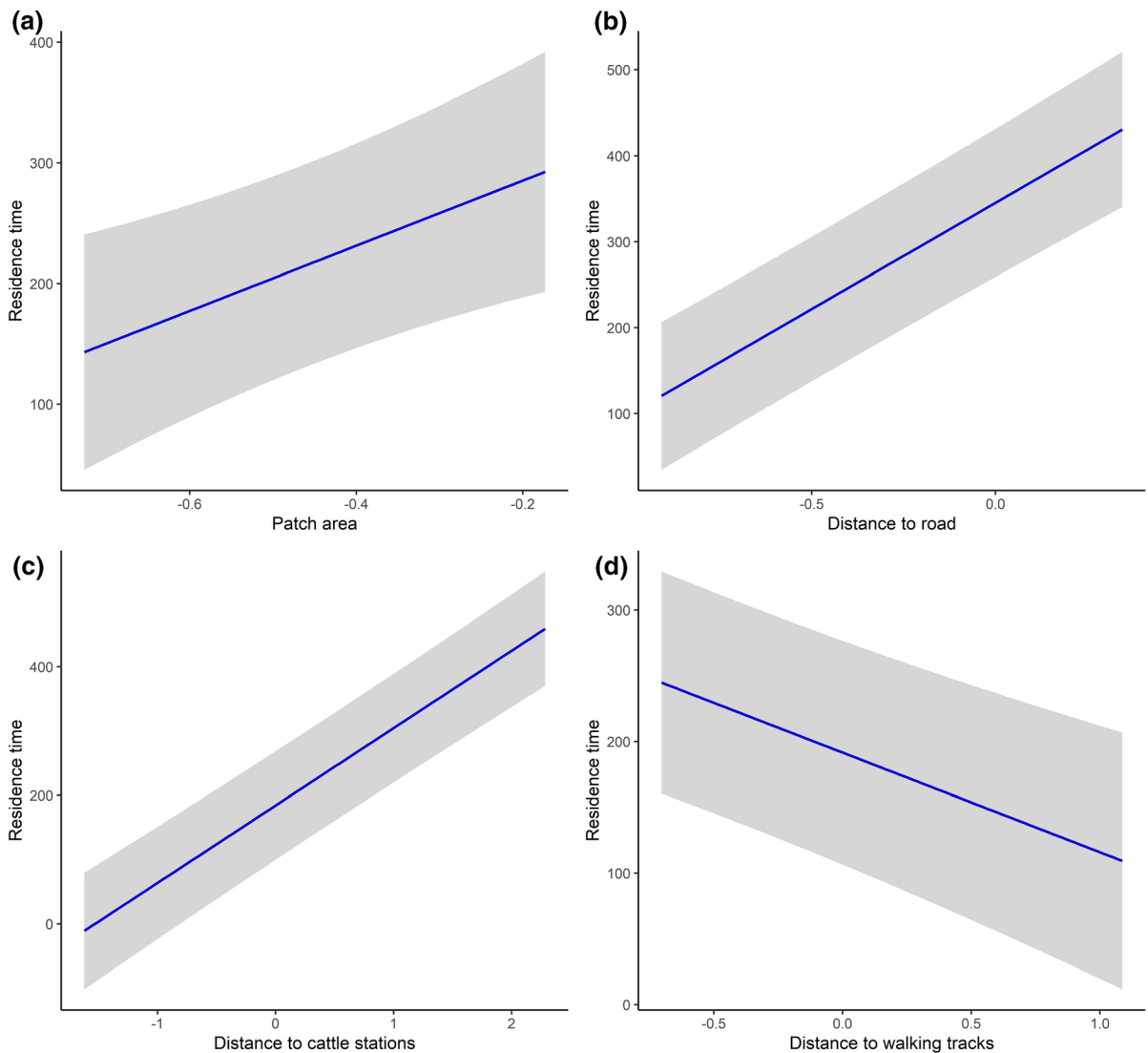


Fig. 3 Estimates of the effect of disturbances and habitat fragmentation on residence time. The blue line represents the trend line with grey ribbon as 95% CI. Red pandas appeared to

spend long hours in **a** large habitat patches; **b** away from roads; **c** away from cattle stations; and **d** close to walking trails

$p < 0.02$). We observed no significant variation in road and track crossing rates by red panda between day and night, nor did the crossing rates differ across the sex class in road ($W = 206$, $p = 0.65$, Wilcoxon rank sum test) and human pedestrian tracks ($W = 172$, $p = 0.57$, Wilcoxon rank sum test). But the track crossing frequency was significantly positively correlated with track density ($r = 0.71$, $p < 0.02$, Fig. S1b) while no significant correlation existed between road crossing and road density (Fig. S1a). We observed no correlation between the frequencies of road and track

crossings and their densities between males and females (Fig. S1c-f).

Temporal pattern of activity level in response to disturbances

In general human activities, livestock presence, dog and vehicle movements peaked at noon throughout the year while red pandas appeared more active during the first half of the day (Fig. 5). Red pandas overlapped more than half of their overall activity level with

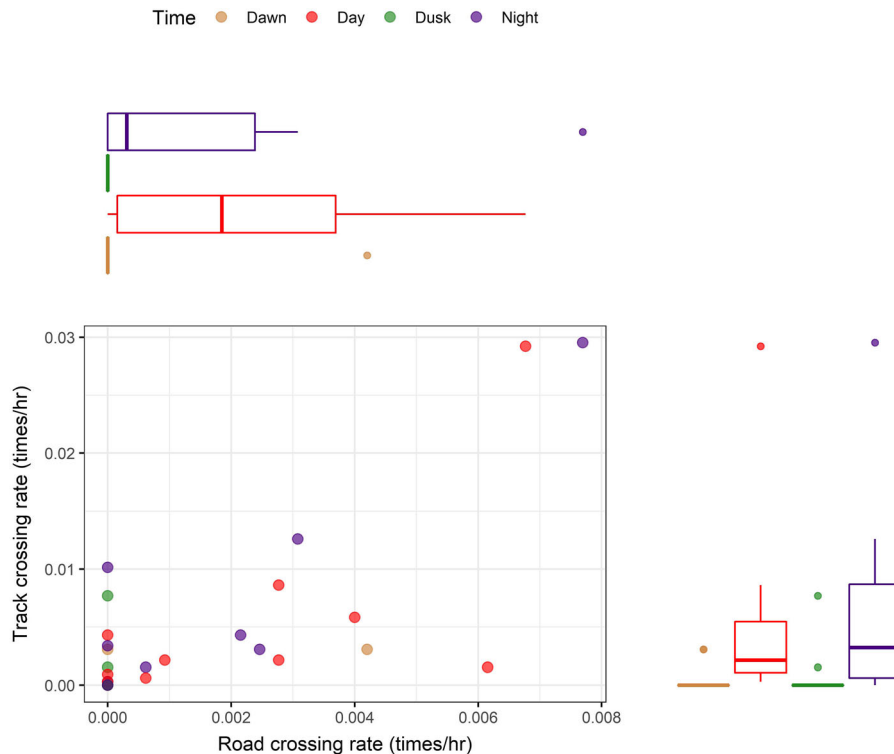


Fig. 4 Scatterplot showing the crossing rate (per hour) of road and tracks by all 10 animals across different times of a diel cycle (day, dawn, dusk and night). Each color represents a specific time of the diel cycle. The plot shows the road and track crossing rates along the x and y axes respectively. Each point represents

the crossing rate of an individual animal at a particular time. Box plots are added on right and top of the scatter plot to show the marginal distribution of road and walking track crossing rates respectively. Points outside the scatter plot depict outliers of the respective box plot

livestock ($\Delta = 0.57$, CI 0.48–0.68), humans ($\Delta = 0.77$, CI 0.68–0.84), vehicles ($\Delta = 0.75$, CI 0.62–0.87), and dogs ($\Delta = 0.74$, CI 0.65–0.83) on a diel cycle. Despite such high overlap their annual activity patterns varied with all these four disturbance sources (Fig. S2). The seasonal activity level of red pandas varied in response to disturbance sources (Fig. S2). Their activity level differed with livestock in the pre-mating ($W = 7.91$, $p < 0.005$) and birthing ($W = 9.32$, $p < 0.001$) seasons, human presence in mating ($W = 7.87$, $p < 0.005$) and birthing ($W = 8.19$, $p < 0.005$) seasons, and dog presence in mating ($W = 4.08$, $p < 0.05$) and birthing ($W = 9.62$, $p < 0.001$) seasons. Red panda's activity level did not vary with livestock ($W = 0.5$, $p = 0.48$) and human presence ($W = 1.03$, $p = 0.31$) in the cub-rearing season. But their activity overlapped with livestock and human presence ranged up to 0.71 (CI 0.43–0.99) and 0.78 (CI 0.51–1) respectively in this

season, while activity overlap in the other three seasons fluctuated between 0.48 and 0.83.

Activity level of red pandas varied in presence of livestock ($W = 4.41$, $p < 0.04$), humans ($W = 4.94$, $p < 0.03$), and dogs ($W = 7.19$, $p < 0.008$) along trails (Fig. 6a–c), and they followed a similar trend in response to livestock ($W = 5.98$, $p < 0.02$) and dogs ($W = 7.1$, $p < 0.008$) only in forest areas (Fig. 6d–f).

Discussion

Our findings suggest that disturbances and habitat fragmentation influence space use and activity patterns of red pandas, but that habitat quality and disturbances determined their home range size. Red pandas partitioned their activity patterns and occupied less risky areas to minimize interaction with disturbance sources. They also avoided disturbed areas and spent long hours in locations away from disturbance

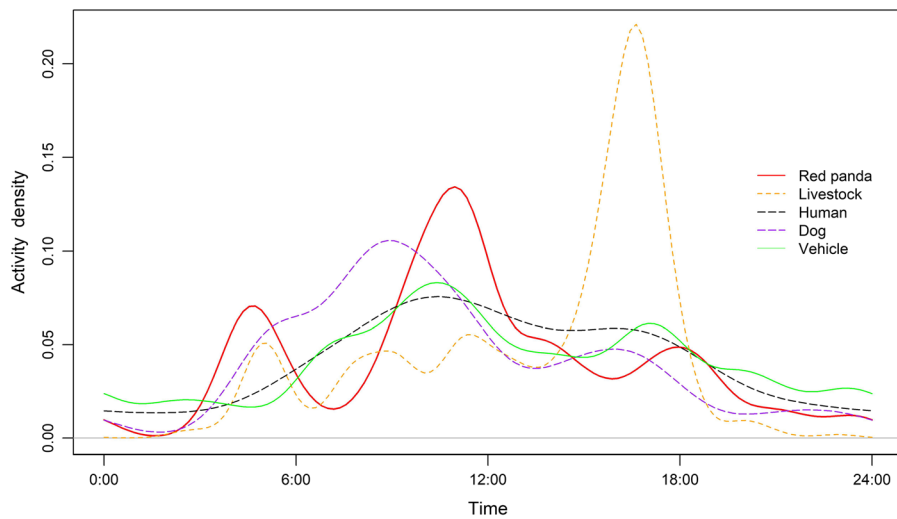


Fig. 5 The annual diel activity density curve of red panda (red line), and potential disturbances: humans (black), livestock (orange), dogs (purple), and vehicles (green). Each curve corresponds to the fitted circular kernel distributions of each animal's activity level

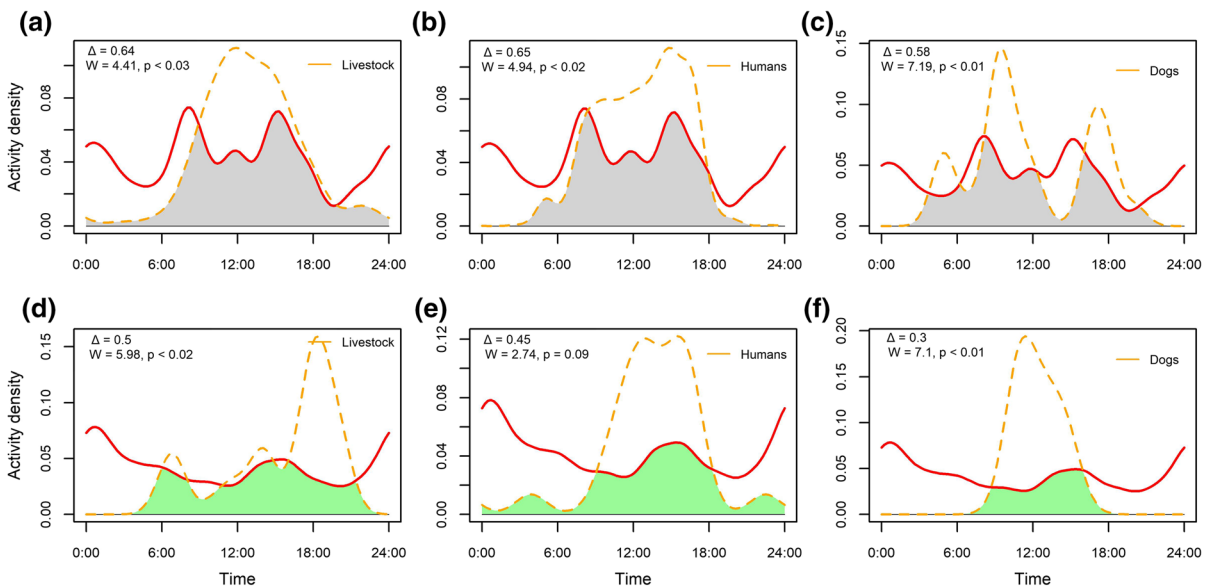


Fig. 6 Temporal overlap activity patterns of red panda (red) and potential disturbances (orange line) along the human-walking trails and forest areas. The Wald test examines the difference in activity patterns between red panda and other

groups at $p \leq 0.05$. The shaded area represents the overlap coefficients (Δ) between each pair. The temporal overlap along the trails (a–c), and forest areas (d–f)

sources except in areas close to pedestrian trails where they partitioned their activity pattern to avoid disturbances.

Our findings partially support the hypothesis that red pandas have larger home ranges in disturbed and fragmented habitat. Red pandas occupied larger ranges in habitat with low forest cover. Their home

range size was smaller while living in areas with high road density. Low forest cover is an indicator of poor habitat quality (Coote et al. 2013). Therefore a larger area is necessary to meet their requirements and maintain social interaction. We also observed some animals having a large home range even when the road density within their range was low. In those cases

forest cover appeared to be more influential in determining home range size. These observations indicate that an intact forest without fragmentation would be ideal habitat for red panda.

Roads usually serve as landmarks of territory marking (Heap et al. 2012). We observed this effect as roads marginally demarcated the home range boundaries of most animals. Further, individuals moved quickly in areas close to roads indicating avoidance behaviour. They slowed down in the vicinity of pedestrian tracks. This result is consistent with the hypothesis that vehicular roads may be a barrier to red panda movement, but tracks are not. There was also a positive correlation between track density and track crossing rate supporting the conclusion that red pandas perceived such linear features as less risky areas. Less traffic along the human-walking trails would have encouraged red pandas to use walking trails more frequently than roads. Red pandas appeared to partition their activity pattern in the vicinity of pedestrian tracks.

The recorded traffic volumes along the road and walking trails must be considered a minimum as during the study period people did not travel due to the COVID-19 restrictions. Road-affected habitats also suffer from habitat loss and high grazing disturbances in human-modified landscapes (Fan et al. 2011; Kang et al. 2014). Animals try to avoid roads for a number of reasons including poor habitat quality, traffic noise, visual disturbance and predators (Harris and Scheck 1992; Jaeger et al. 2005; Coffin 2007). Most importantly wildlife perceives human related features as risky (Frid and Dill 2002) and this may have discouraged red pandas from visiting roadsides. A similar effect of road and habitat quality on home range has been reported in other species (Jerina 2012; Tucker et al. 2018). The study area was experiencing travel restrictions due to COVID-19 during the study period. Therefore, the effect of traffic volume on red panda is likely to be more pronounced during normal times.

Acquiring the habitat that meets animal's needs for food, rest, and avoidance of predators and human disturbance is challenging (Martin et al. 2010). Therefore wildlife avoids disturbances and human-proximity by partitioning their activity pattern (Hebblewhite and Merrill 2008) and occupying less risky areas (Rode et al. 2006; Martin et al. 2010). Our findings are in line with predation risk hypothesis (Frid and Dill 2002) and there is evidence consistent with

red pandas perceiving humans, dogs, livestock and vehicles as disturbances; they adapted to these disturbances by partitioning activity patterns and occupying less disturbed habitat patches.

The variation in road and track crossing rate across the diel cycle shows that red pandas avoid crossing such features during dawn and dusk. This could be explained by time allocation behaviour for different activities to minimize risk (Brown 1999). Red pandas actively forage at dawn and dusk while they travel long distances during the day and night to access ecologically key areas located apart. We also observed predators being more active during dawn and dusk (Fig. S3), and roads and trails can serve as ecological trapping sites for these predators (Forman and Alexander 1998). Prey has to cross such features with the trade-off of energetic cost between the time spent to become vigilant and foraging (Brown 1999; Ciuti et al. 2012b). For this reason, red pandas may have opted to avoid risky areas and stay in a feeding patch during dawn and dusk.

Red panda's response level varied across disturbance sources and their volume. In general, the disturbance sources were primarily active during the day while red pandas remained highly active in the early morning hours with minor peaks at dawn and dusk. They were flexible and exhibited seasonal variation to cope with some disturbances, but they seemed to be more sensitive in the birthing season. This observation also supports the hypothesis of risk avoidance by activity partitioning (Creel et al. 2008).

The threat level was high in the mating season because red pandas spend more time on the ground. For this reason they became more active during the dawn to avoid interactions with human and dogs. In the birthing season they altered their activity pattern and became active throughout the diel cycle but avoided humans and dogs during their peak activity hours. They followed a similar trend in the cub-rearing season but did not show a marked response to disturbances. Food availability is high in the monsoon and post-monsoon seasons which overlaps with birthing and cub-rearing seasons respectively. Dense vegetation provides high cover and makes the forest ideal for hiding (Wevers et al. 2020). Additionally, red pandas occupied the least disturbed habitat patches during these seasons which minimizes their encounters with disturbances. These attributes encourage them to remain active during the day.

Red pandas' partitioning of activity pattern shows their adaptation to coexist with predators and disturbances. They partitioned their activity pattern along the human-walking trails and forest areas and avoided livestock and dogs. But their response to human presence differed in walking trails and forest as their activity pattern did not vary in the presence of humans in forest areas. This could be attributed to low human traffic in forest areas (0.04 people/day) in comparison to higher traffic along the trails (2.27 people/day).

We acknowledge that there may be some error in overlap estimation due to the use of data obtained from two different sources: camera and telemetry data (Lashley et al. 2018). However, there is probably no other way to gather such data and if error does exist it is likely to be small given the small proximity thresholds we used.

We recorded six cat species (Bista et al. 2021a) and three other predators in the study area which were nocturnal except the yellow-throated marten *Martes flavigula* and Himalayan black bear *Ursus thibetanus* (Fig. S3). The variation in activity patterns between red panda and these carnivores show that presence of predators may have initially shaped red panda's diurnal activity pattern with minor peaks during the early morning and evening hours (Wu et al. 2018; Higdon et al. 2019). Their arboreality also helps them avoid predation risk but we have insufficient data from other sympatric predators to reach firm conclusions. Therefore our findings warrant further study to understand red panda's response to predators.

Red pandas showed site fidelity in areas away from disturbances which could be an adaptation to adjust in a human-modified landscape. Areas close to roads, cattle stations and settlements are risky and characterized by poor habitat quality in terms of food availability and resting and hiding sites (Coffin 2007; Schieltz and Rubenstein 2016). The energetic cost to accommodate such poor-quality habitat is high (Frid and Dill 2002). For this reason red pandas may have opted to occupy areas away from such disturbances. However, the number of revisits and residence time in areas close to human trails did not decrease. The study area had relatively high trail density which probably did not leave an option to stay away from such trails. They appeared to have adapted along the pedestrian features by partitioning their activity patterns to avoid encounters with disturbance sources. Additionally, trails had low traffic volume and noise, narrow open

space and less disturbed vegetation. For this reason, red pandas may have remained in these areas with the expenses of minimal energetic cost.

Conservation implications

This study demonstrates that GPS telemetry coupled with camera trapping can be used for evaluating the effect of disturbances and habitat fragmentation on arboreal mammals. These results have implications for the conservation of the red panda and other diet and habitat specialist species, such as giant panda *Ailuropoda melanoleuca* (Swaisgood et al. 2016), koalas *Phascolarctos cinereus* (Woinarski and Burbidge 2020), tree kangaroos *Dendrolagus* spp. (IUCN 2021b) and some species of bamboo lemurs (IUCN 2021a).

This study presents evidence consistent with the barrier effect of roads on movement of red pandas. It appears that red pandas can adapt to habitat fragmentation and disturbances to some extent but they may be susceptible to local extirpation in fragmented and degraded habitat. Increase in road density and traffic load can fragment the habitat, discourage movement across such linear features, and interfere in conspecific interactions resulting in population isolation. The trade-off between occupying such habitat and adaptation in disturbed areas can lead to increased risk of mortality and population decline in the long run. This fact underpins the need to minimize human-induced disturbances in red panda habitat. Human activities should be strictly regulated during the biologically crucial seasons: mating and birthing seasons. Conservation programs should focus on identifying ecologically sensitive areas, maintaining habitat continuity, and minimizing disturbances due to road and livestock herding. We suggest avoiding road construction in most, if not all, ecologically critical sites. In unavoidable cases, restrictions on vehicle's speed and noise should be maintained, and wildlife crossings should be built in high-risk areas.

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Authors' contributions Conceived ideas, designed methodology, analysed and interpreted the data, and led the writing of the manuscript—DB. Collected data—DB, STL. Supervision: GSB, NJH, PJM. Contributed critically to revising the manuscript—DB, GSB, NJH, PJM. Read and approved the final manuscript: DB, GSB, NJH, STL, PJM.

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Data availability The datasets generated and/or analysed during the current study are not publicly available due to the risk of poaching but are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethical approval 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).

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