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Avoidance or Coexistence? The Spatiotemporal Patterns of Wild Mammals in a Human-dominated Landscape in the Western Himalaya

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Human–wildlife interfaces are increasing rapidly due to the disproportionate growth of human and wildlife populations in a spatial context. The Himalayan system, a global biodiversity hotspot, is subject to landscape modification from various anthropogenic activities. In this study, we offer insights into the human–wildlife interface, reflecting avoidance or coexistence, with implications for local and landscape management strategies. We investigated fine-scale space use and temporal activity patterns of mammalian wildlife in a human-dominated landscape, outside a protected area. The research methods involved robust digital camera trap sampling (n = 131) across the target area (116 km^2) with a total human population of 153,585. We developed a new sampling strategy that accounted for spatial heterogeneity in the habitats and variations in mammalian community composition. Our results showed that, in spite of high usage and the presence of humans across the study area, 16 wild mammal species used the area with varying intensities, exploiting habitat and forage availability. Of the camera traps placed in the study area, 70.23% had overlapping captures for humans on foot and wild mammal species. Generalist species used natural, modified, and altered habitats, while herbivores remained in natural and modified areas. However, some mammals that used modified/altered areas avoided humans by modifying their temporal activity. In the context of management of large landscapes, including areas outside the protected area network, the results of this study highlight the significant plasticity exhibited by wild mammals in negotiating natural and human-modified habitats. This offers an opportunity to develop conservation management strategies focusing on these fine-scale patterns and human actions.

Keywords: *agricultural landscapes; animal behavior; Himalaya; human–wildlife interface; landscape management; activity pattern.*

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Introduction

Human population growth and related modification and loss of natural habitat continue to pose a serious threat to biodiversity (Noss et al 1996; Wilcove et al 1998; Western 2001; Tigas et al 2002). Due to alterations in land-use types and growing human populations around protected areas (PAs), these natural areas are becoming increasingly isolated patches (Wittemyer et al 2008). Hence, a landscape-level conservation approach that is ecologically representative and socially inclusive is needed. Many recent studies have focused on the role of agricultural landscapes, also termed anthropogenic landscapes, in the conservation of different taxa and have revealed their importance in conservation (Pimentel et al 1992; Harvey et al 2008). The biodiversity has been attributed to the habitat heterogeneity that such areas provide (Benton et al 2003; Bennett et al 2006; Gardner et al 2009; Anand et al 2010). This led the Convention on Biological Diversity (CBD) to issue Aichi Biodiversity Target 7, which focuses on the sustainable management of agroecosystems to conserve biodiversity. The CBD also proposed the concept of "Other Effective Area-based Conservation Measures" to achieve Aichi Biodiversity Target 11, which aims to protect 17% of terrestrial area to promote landscape conservation, particularly in biodiversity-rich areas, such as the Himalaya (CBD Plan 2011–2020; CBD 2018).

Studies in anthropogenic landscapes have suggested that relatively more adaptable species can live in a matrix of natural and human-dominated habitats (Macdonald 1979; Fedriani et al 2001; Fuller et al 2010; Rodewald and Gehrt 2014) and show more tolerance of human-mediated disturbance (Doncaster and Macdonald 1991; Tigas et al 2002).

The current trend of conservation discourse highlights the importance of landscape management, and hence the need to assess the importance of areas outside PAs. About 90% of tropical forests lie outside the PA network (WWF 2002) and are threatened by continual pressures of habitat modification and deforestation (DeFries et al 2005). Most studies conducted outside PAs are from North America, in and around the United Kingdom, and Australia (Tigas et al 2002; Beckmann and Berger 2003; Contesse et al 2004; Ditchkoff et al 2006; Newsome et al 2014); a few are from other regions of the world (Abay et al 2011; Athreya et al 2013). In India, however, little is known about the ecology of mammals found in proximity to human habitations. Most studies have focused on the negative interactions (Treves and Karanth 2003; Bhatia et al 2013; Naha et al 2018, 2019), with very few examples of the habitat-use patterns of wildlife in agricultural landscapes (Kumara et al 2004; Athreya et al 2013; Banerjee et al 2013; Ghoshal et al 2016). Some studies showing the importance of a matrix of forested and unforested areas have been conducted in different parts of India but are mostly restricted to birds (Elsen et al 2017), invertebrates (Dolia et al 2008; Anand et al 2010), and plants (Rawat et al 1999).

The Indian Himalayan region has a network of 138 PAs, covering 10.3% of the geographical region (WII NBWL, 2020), with a total forest cover of 33.7% (FSI 2017). Some of these are managed by local communities and are termed *van panchayat* (Agrawal 1999). Forests interspersed with human habitations are potential wildlife habitats outside PAs (Cuiti et al 2012). As a world biodiversity hotspot, holding 66% of Indian mammalian diversity (Chandra et al 2018), it is important to understand the significance of areas outside the PAs in the Indian Himalayan region.

Animals living in proximity to human-dominated landscapes are known to alter their behavior spatially and/or temporally (Graham et al 2009; Cuiti et al 2012; Valeix et al 2012; Carter et al 2015). In a region such as the Himalaya, we hypothesized that in order to use human-dominated landscape, wild animals would negotiate human presence in space and/or time to avoid direct encounters with humans. We carried out this study to understand the spatiotemporal patterns in wildlife populations using the human-dominated landscape of the Western Himalaya. Following Gardner et al (2009), we defined modified areas in our study as former native vegetation areas that have not been significantly altered to urban areas but to land uses such as agriculture, orchards, and settlements. We designed a sampling protocol to take into account all land-use types and the sampling biases that may generally occur in mountainous landscapes to investigate this idea.

Materials and methods

Study area

We carried out this study in the Mandal valley (area: 116 km^2; 30°22′–30°30′N; 79°13′–79°21′E), a mid- to high-elevation (900–3400 meters above sea level [masl]) Himalayan area in the state of Uttarakhand, northern India (Figure 1). The Mandal valley touches the southern boundary of the Kedarnath Wildlife Sanctuary. This region provides access to Hindu shrines and tourist destinations in the region. A road connecting the famous Hindu shrines Kedarnath and Badrinath passes through this area, resulting in high vehicular traffic during May to October. Two Hindu shrines, Tungnath (3500 masl) in the northeast of the study area and Rudranath (3400 masl) in the northwest, attract significant numbers of pilgrims and tourists. Figure 2 shows the main land uses in the study area.

The study area is a densely populated, with a matrix of 11 urban and 35 small and large rural habitations (DCOU 2011), including the district headquarters, Gopeshwar/Chamoli. This provides a gradient of human disturbance levels based on village/town type and human population density. Figure 3 shows the distribution of humans in the study area: They are not restricted to settlements and agriculture but instead are spread across the study area. The total human population within the intensive study area was 153,585 (DCOU 2011).

Kedarnath Wildlife Sanctuary (975 km^2) has a wide diversity of mammalian fauna, most notably, mountain ungulates and large carnivores (Sathyakumar 1994). Local people are mostly dependent on forest resources and agriculture as their main sources of livelihood and include a few pastoral communities. Pressure from lopping and cutting varies in different *van panchayat* forests. However, the majority of the villagers, as observed during the study, value forests and are aware of their importance. They were also positive about conservation of wildlife and would agree to coexist if the harm caused by wild animals was stopped (personal observation, N. Srivastava).

Within the Mandal valley, we selected an intensive study area that ranged from 900 masl to 2500 masl with a diversity of land-use/land-cover types. Based on the objectives of this study, we deployed cameras up to 2500 masl; human settlements are not present above this.

Study design

The study area has high habitat heterogeneity, and, in order to cover the landscape configuration, we plotted grids of 1 km^2 in the study area. The heterogeneous landscape includes protected forests; *van panchayat* forests, which are dense to open and disturbed, due to lopping and grazing pressure; degraded/abandoned lands that have been taken over by scrub species, such *Lantana camara*, *Rubus* spp, *Berberis* spp, and others; agricultural areas; and human settlements. We placed camera traps with a minimum of 1 to maximum of 3 traps per grid based on habitat heterogeneity in the grid. Within a grid, the area was intensively searched for wild animal signs (droppings/tracks/scent marks) and for resources (crop fields, water). In crop fields, trails leading to forests and/or connecting two villages were chosen to optimize captures. Camera trap locations were selected after 45 days of reconnaissance. Sampling was done once per grid without repetitions, shifting cameras to other grids after each session (mean sampling days = 15) from lower elevations (January 2017 onwards) to higher elevations (April 2017 onwards) to maintain temperature effects. This approach of placing camera traps in human-dominated mountain areas has not been attempted before and, hence, can be considered a model to be tested for its efficacy in such landscapes.

Field methods

In total, 131 camera trap points were sampled with 40 Cuddeback C1 camera traps, covering areas from the most highly populated towns to the smallest villages (within the study area), as well as agricultural fields, protected and unprotected forests and orchards, garbage dump sites, planted forests, and fallow land. Given the mountainous terrain and fine-scale sampling, most locations were not accessible by road; accordingly, the study involved a

FIGURE 1 Map of the Mandal river subbasin (intensive study area). Kedarnath Wildlife Sanctuary (WLS) is situated in the north of the study area.

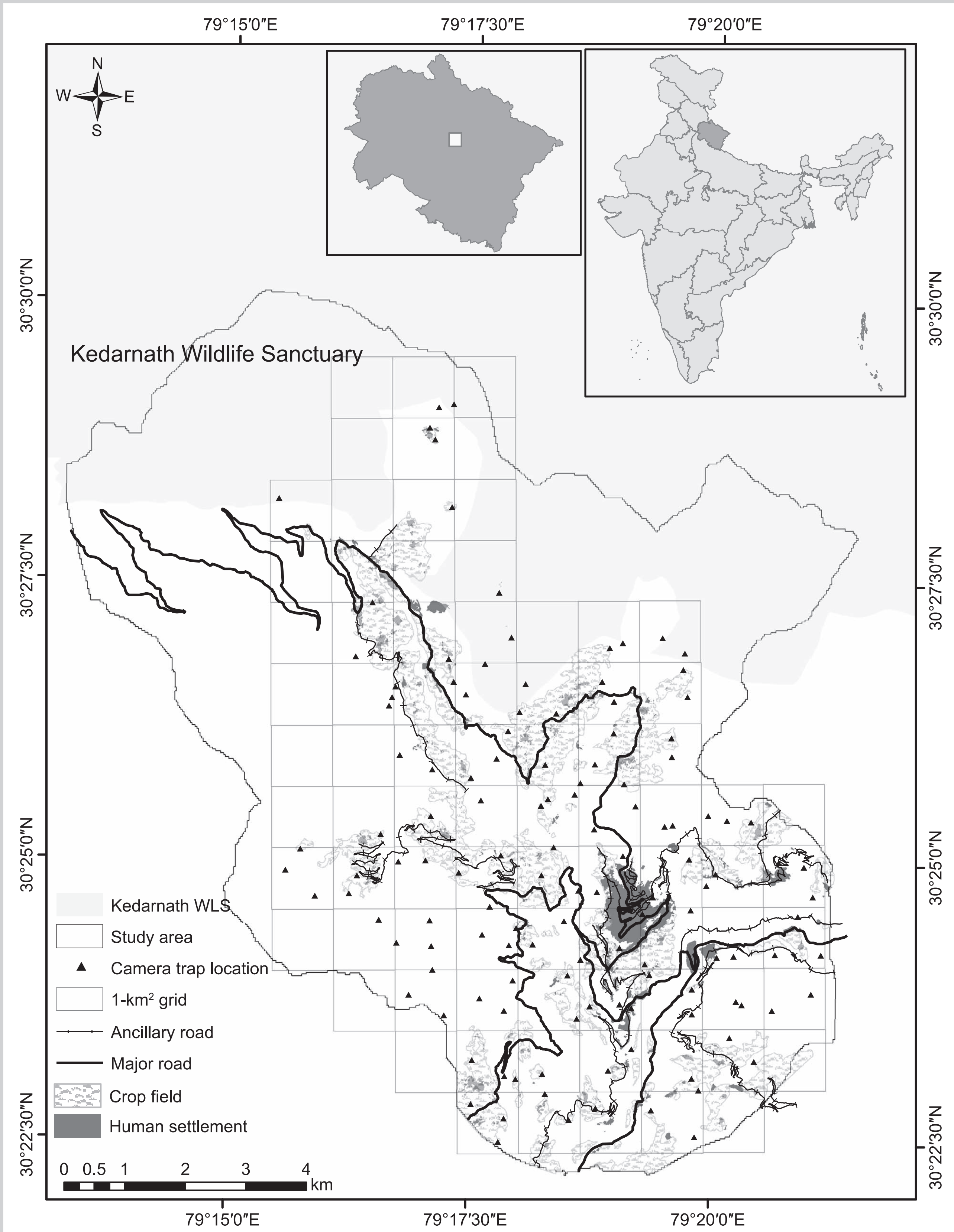

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FIGURE 2 Land-use map of the study area. We used Sentinel 2A data acquired on 28 March 2017, tile no. T44RLU. The accuracy assessment was 75% for supervised and 66.2% for unsupervised classification (kappa statistics can be found in Appendixes S2 and S3, respectively; *Supplemental material*, https://doi.org/10.1659/MRD-JOURNAL-D-19-00046.1.S1). Shape files used for agriculture and settlements were manually digitized using Google Earth Pro and were overlaid on the classified shape file.

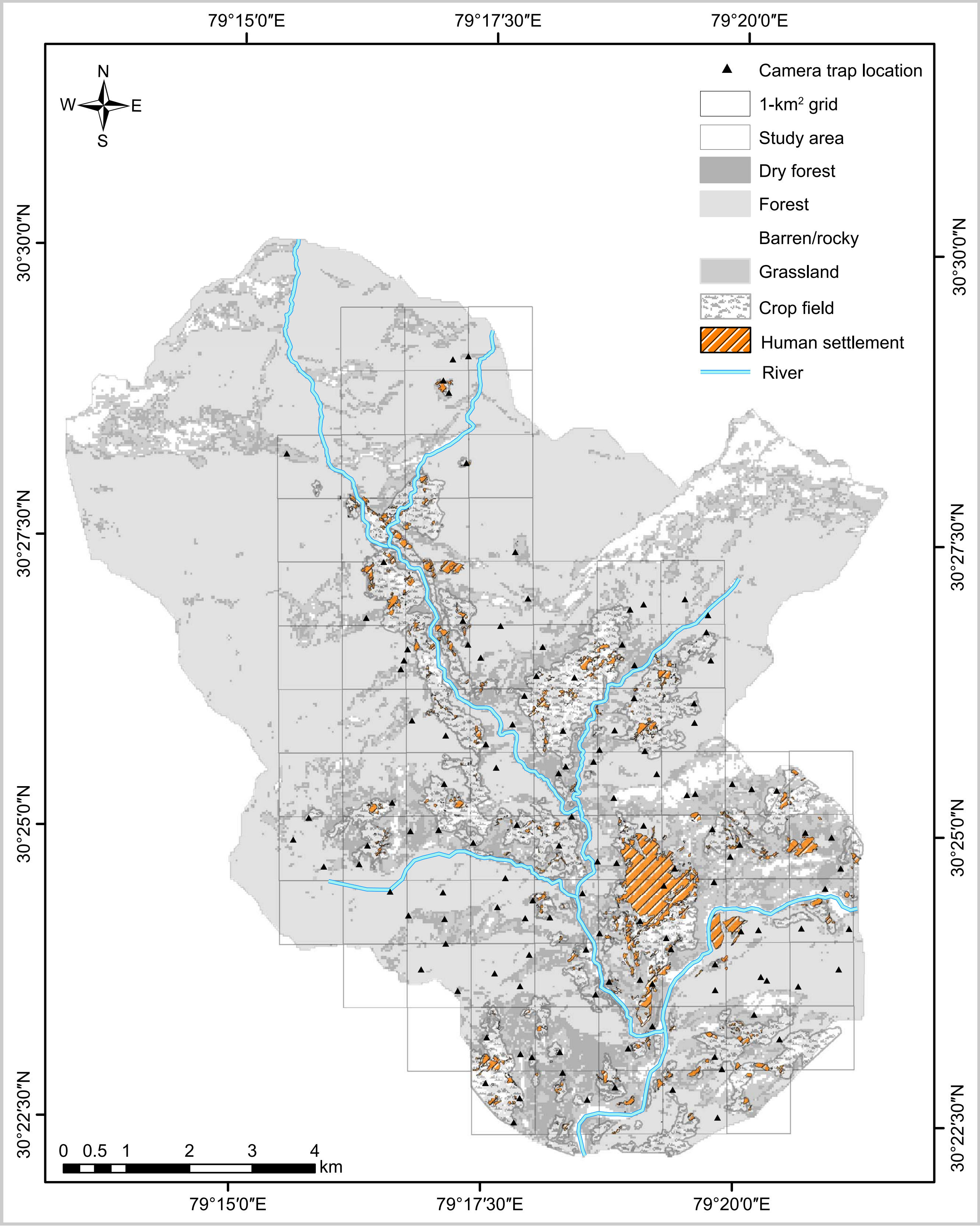
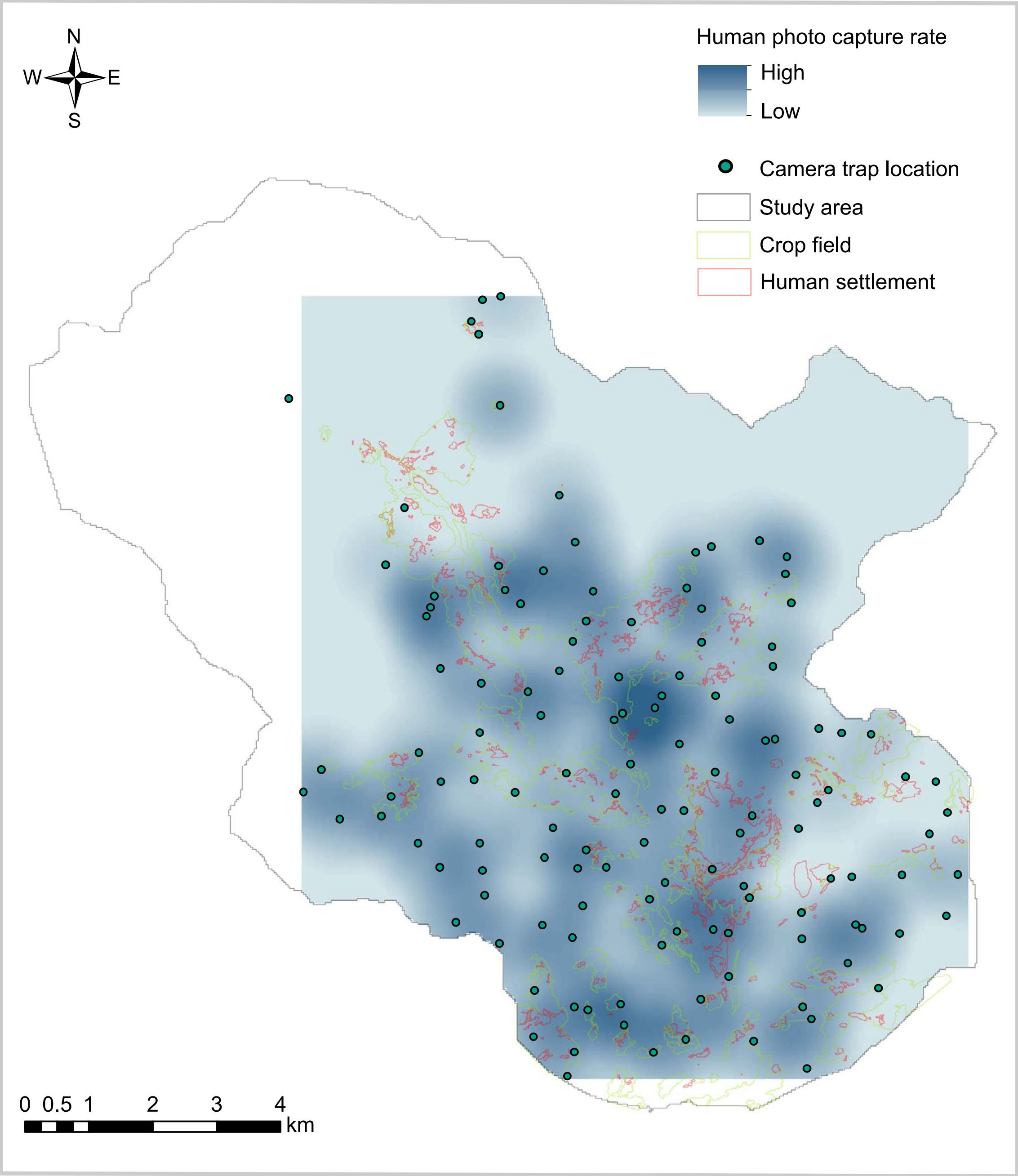


FIGURE 3 Heat map representing the distribution of humans in the study area based on a kernel density estimate.



substantial amount of walking (∼1300 km). After a month of reconnaissance, camera traps were placed strategically and were set to capture photographs at 5 second intervals to maximize detection. At certain points, where the probability of false captures was high, the time interval was set to 10–15 seconds. Camera traps were placed 2–3 m above the ground to avoid vandalism. The cameras were adjusted in a way that covered the area of focus (eg animal trail) and were checked for detection sensitivity to ensure functioning. This was done by putting the camera on test mode and walking on the trail at different heights, as per study mammals heights. We did not use baits for our study. Photos captured after 5 minute intervals were selected for analysis in order to minimize chances of redundancy and reduce the possibility of biased photo capture rates for camera traps with a 10–15 second interval between captures. We categorized six land-use types: settlements, crop fields, mosaic, fallow lands, dry forest, and moist forest. The criteria set for each habitat type are provided in Appendix S1 (*Supplemental material*, https://doi.org/10.1659/MRD-JOURNAL-D-19-00046.1.S1).

Analytical methods

A matrix of camera traps with habitat types was constructed for all species in MS Excel 2016, and mean and standard errors of photo capture rate per 100 trap nights were calculated for each wild species in different habitat types. In order to visualize the distribution of humans in the study area, we interpolated photo capture rates of humans and created a heat map. We used the software ArcMap 10.6.1 to

TABLE 1 List of mammal species photo-captured along with overall photo capture rate and number of photo captures recorded in Mandal river sub-basin (January 2017–May 2017).

Species name	Overall photo capture rate (no./100 trap nights) [Total no. photo captures]
Indian crested porcupine (*Hystrix indica*)	12.16 [236]
Sambar (*Rusa unicolor*)	9.17 [178]
Rhesus macaque (*Macaca mulatta*)	8.66 [168]
Barking deer (*Muntiacus muntjak*)	8.60 [167]
Wild pig (*Sus scrofa*)	7.83 [152]
Himalayan langur (*Semnopithecus schistaceus*)	6.75 [131]
Common leopard (*Panthera pardus*)	2.37 [48]
Leopard cat (*Prionailurus bengalensis*)	2.16 [42]
Himalayan palm civet (*Paguma larvata*)	2.16 [42]
Red fox (*Vulpes vulpes*)	1.55 [30]
Himalayan grey goral (*Naemorhedus goral bedfordi*)	1.55 [30]
Jungle cat (*Felis chaus*)	1.49 [29]
Himalayan serow (*Capricornis thar*)	1.13 [22]
Yellow-throated marten (*Martes flavigula*)	1.08 [21]
Golden jackal (*Canis aureus*)	0.15 [3]
Asiatic black bear (*Ursus thibetanus*)	0.05 [1]

create kernel density plots, using log-transformed capture rates. We overlaid the shape files of settlements and agriculture fields (digitized manually using Google Earth Pro imagery, where polygons were drawn around agricultural fields and settlements using the add polygon tool) over the map to understand the distribution of humans in the human-modified landscape.

Time stamping in each photo capture was used to estimate temporal activity patterns. For this analysis, time of photo captures was used and divided into two broad habitats, natural habitats and modified habitats, which included fallow land, mosaic habitats, crop fields, and settlements. Most of the modified areas were also close to human settlements, and it was expected that animals would show differences in activity patterns between the areas.

We used R studio, package camtrapR (Niedballa et al 2016), to summarize information on date and time and created a capture matrix for all species. Circular statistics that examined the temporal pattern of animal captures, reflecting time-specific behavioral responses of the species, were calculated and plotted using ORIANA software version 4 (Kovach 2011). For angular data, such as time, we conducted a nonparametric Watson U^2 test (Zar 1999), which was used to compare two sets of data using mean square deviations. We did this to see if our study species had significant difference in temporal activity patterns between natural and human-modified areas. We tested for temporal overlap between wild animals and humans by plotting the time of photo captures using MS Excel. This was done for the overall study area for diurnal and nocturnal species as found in our study. We went on to explore fine-scale temporal overlap/avoidance in natural, modified, and settlement areas. For temporal analyses, we used the raw data of photo capture (ie no time interval was considered; the 5 minute interval was used for other analyses), as our objective was to look at overlap. We plotted kernel density plots using R 3.4.2 (R Core Team 2014). These plots helped to estimate the coefficient of overlap between the two data sets using the von Mises kernel for circular distributed data (Meredith and Ridout 2014).

Results

Spatial pattern

We recorded 16 species of wild mammals using the study area, despite the high ($n = 3733$) presence of humans across the land-cover/land-use types (Figure 3). The mean number of sampling sessions in the study area was 14.82 ± 0.67 trap nights. The number of photo captures of each species is listed in Table 1. Golden jackal (*Canis aureus*) and Asiatic black bear (*Ursus thibetanus*) had low photo captures ($n = 3$ and $n = 1$, respectively) and hence were excluded from further analyses. We found that 70.23% of the camera traps had overlapping captures for humans on foot and wild species. There were species-specific variations in the capture rates in different habitat types in the study area. The mean values of log-transformed photo captures per 100 trap nights are presented in Table 2. The two primates showed different habitat-use patterns: While rhesus macaques (*Macaca mulatta*) showed high usage in areas near human settlements (0.73 ± 0.88) and in fallow land (0.46 ± 0.93), Himalayan langurs (*Semnopithecus ajax*) were never captured in fallow land and

TABLE 2 Mean capture rates (number of captures/100 trap nights, log transformed) of wild mammals in different habitat types of Mandal river subbasin (December 2016–April 2017).

Species	Habitat type (mean ± SD)					
	Settlement	Crop field	Mosaic	Fallow land	Dry forest	Moist forest
Himalayan langur	0.26 ± 0.76	0.20 ± 0.58	0.23 ± 0.42	0.00	0.19 ± 0.47	0.25 ± 0.55
Rhesus macaque	0.73 ± 0.88	0.28 ± 0.60	0.16 ± 0.40	0.46 ± 0.93	0.06 ± 0.28	0.06 ± 0.26
Golden jackal	0.07 ± 0.28	0.06 ± 0.23	0.00	0.00	0.00	0.00
Himalayan masked palm civet	0.07 ± 0.28	0.29 ± 0.57	0.17 ± 0.41	0.08 ± 0.25	0.02 ± 0.10	0.15 ± 0.42
Jungle cat	0.13 ± 0.37	0.36 ± 0.69	0.11 ± 0.32	0.17 ± 0.35	0.00	0.02 ± 0.12
Leopard cat	0.14 ± 0.44	0.13 ± 0.36	0.06 ± 0.26	0.30 ± 0.46	0.16 ± 0.46	0.20 ± 0.40
Red fox	0.00	0.15 ± 0.41	0.11 ± 0.37	0.00	0.14 ± 0.33	0.11 ± 0.37
Yellow-throated marten	0.10 ± 0.31	0.05 ± 0.22	0.09 ± 0.26	0.07 ± 0.20	0.04 ± 0.19	0.15 ± 0.39
Barking deer	0.00	0.33 ± 0.53	0.57 ± 0.78	0.36 ± 0.72	0.23 ± 0.49	0.52 ± 0.65
Himalayan grey goral	0.00	0.09 ± 0.35	0.00	0.00	0.34 ± 0.47	0.18 ± 0.41
Sambar	0.00	0.62 ± 1.04	0.28 ± 0.62	0.00	0.04 ± 0.18	0.21 ± 0.53
Himalayan serow	0.00	0.09 ± 0.35	0.00	0.00	0.04 ± 0.21	0.11 ± 0.36
Wild pig	0.12 ± 0.35	0.29 ± 0.71	0.70 ± 0.73	0.47 ± 0.50	0.18 ± 0.50	0.32 ± 0.54
Indian crested porcupine	0.42 ± 0.64	0.53 ± 0.67	0.84 ± 0.70	0.92 ± 0.74	0.48 ± 0.71	0.53 ± 0.64
Asiatic black bear	0.00	0.00	0.00	0.00	0.05 ± 0.26	0.00
Common leopard	0.09 ± 0.27	0.06 ± 0.23	0.30 ± 0.48	0.39 ± 0.63	0.11 ± 0.38	0.21 ± 0.47

had high usage of natural habitats, both dry (0.19 ± 0.47) and moist (0.25 ± 0.55). Small- to medium-sized carnivores were captured in almost all habitat types, except for red foxes (*Vulpes vulpes*), which were never captured in areas near human settlements and fallow land. We observed an interesting trend of ungulates avoiding areas near human settlements, except wild pig (0.12 ± 0.35). Goral (*Naemorhedus goral bedfordi*) and serow (*Capricornis thar*) were never captured in other disturbed areas, such as mosaic and fallow land, except for one instance for each, in crop fields. Indian crested porcupine, a rodent, was photo captured in all habitat types with similar frequency and was also the most frequently photo-captured species among all wild mammals ($n = 236$). Leopards used all habitat types, though they were photo-captured relatively more in mosaic (0.30 ± 0.48), fallow land (0.39 ± 0.63), and moist forest (0.21 ± 0.47).

Temporal pattern

Rose diagrams of temporal activity for study species are presented in Figure 4. In cases where the line indicating standard deviation is red, deviation from the expected directionality was wider than expected. Results of the Watson U^2 test showed that species such as Himalayan masked palm civet, red fox, yellow-throated marten, and barking deer showed no significant difference in temporal activity pattern between the two habitats. Other species, such as Himalayan langur (0.74, $P < 0.001$), rhesus macaque (0.33, $P < 0.005$), wild pig (0.58, $P < 0.001$), and Indian crested porcupine (0.38, $P < 0.005$), showed a significant difference in their temporal activity between the two habitats. While there was no significant difference in usage between the two habitats by common leopard (*Panthera pardus*), leopard cat (*Prionailurus bengalensis*), and sambar (*Rusa unicolor*), it is interesting to note that these species had an altered peak activity period after midnight in modified areas (Figure 4). Jungle cat, serow, and goral were captured only once in either habitat, and so a difference in temporal pattern could not be determined. However, others that did not show a significant difference in temporal activity between natural and modified areas showed different activity peaks in the two habitat types (Figure 4). The average period of daylight during the study was 7:00 h to 18:00 h.

The temporal-overlap graphs for human and wild species (diurnal and nocturnal) (Figure 5) show that the activity of diurnal species, such as langur, macaque, barking deer, goral, and marten, overlapped with human activity; however, barking deer was also found to be active in nocturnal hours. The human–animal temporal overlap (Table 3) highlights the observation that nocturnal animals such as wild pig (Dhat value = 0.04), sambar (0.04), common leopard (0.04), and jungle cat (0.04) had minimal temporal overlap with humans in settlements, though this was not significantly different from other land-use types. Hence, these animals have adapted to avoid direct encounters with humans, but they still access these areas for resources. Except for langur (Dhat value = 0.44, 0.39 modified and settlement habitats, respectively), macaque (0.57, 0.61), barking deer (0.62 in modified habitat), and yellow-throated marten (0.45 in modified habitat), all other species had a significantly low overlap percentage in modified and/or settlement areas.

FIGURE 4 Temporal rose diagrams of wild animals in natural (f) and modified (nf) areas.

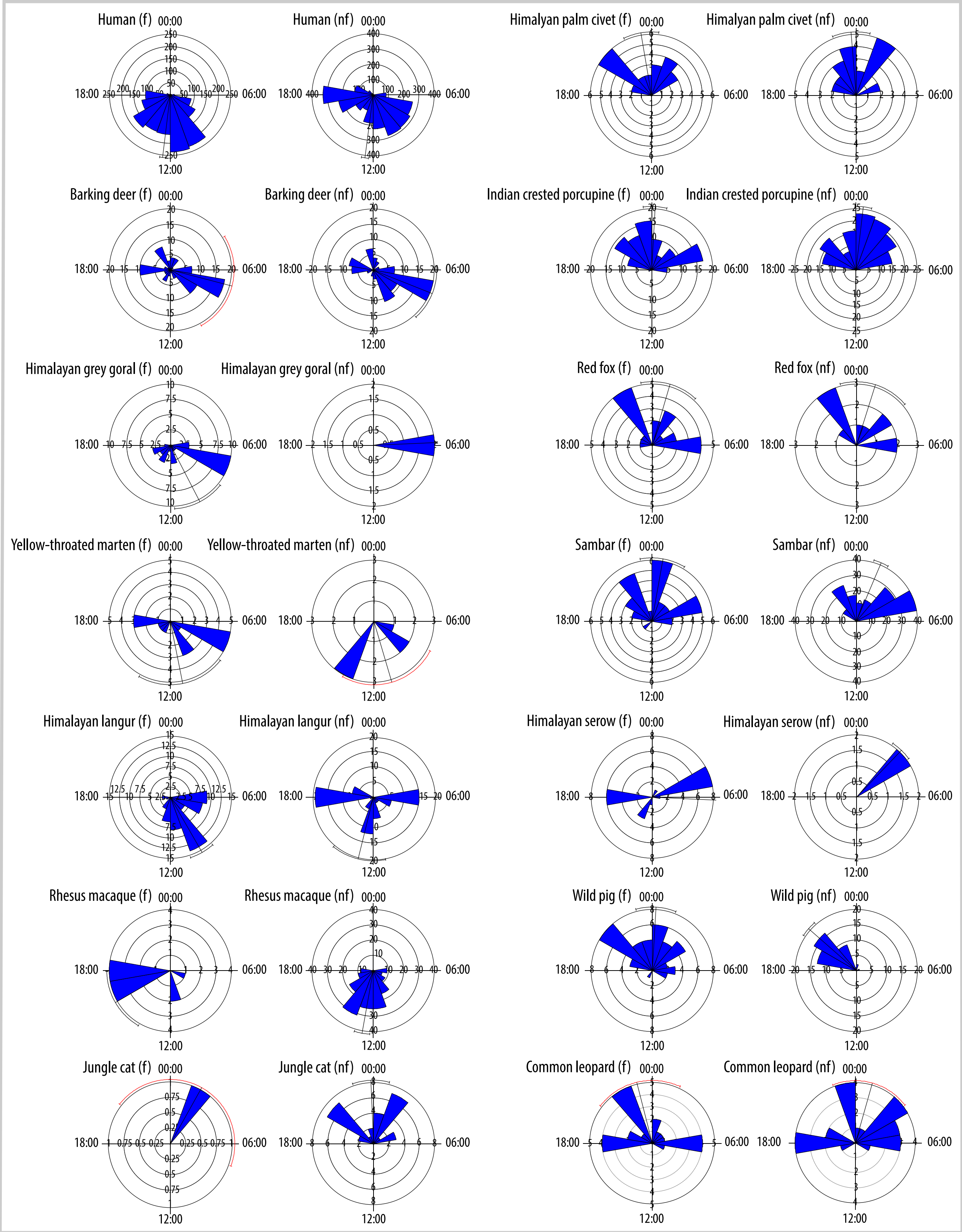


TABLE 3 Temporal overlap of wild mammals with humans in three habitat types of Mandal river subbasin (December 2016–April 2017).

Species	Habitat	Sample size	Dhat value
Himalayan langur	Natural forest	55	0.73
	Modified	29	0.44
	Settlement	47	0.39
Rhesus macaque	Natural forest	55	0.51
	Modified	76	0.57
	Settlement	81	0.61
Barking deer	Natural forest	82	0.42
	Modified	85	0.62
	Settlement	0	NA
Himalayan grey goral	Natural forest	28	0.66
	Modified	2	NA
	Settlement	0	NA
Sambar	Natural forest	29	0.09
	Modified	149	0.04
	Settlement	0	NA
Himalayan serow	Natural forest	20	0.40
	Modified	2	NA
	Settlement	0	NA
Wild pig	Natural forest	42	0.16
	Modified	106	0.12
	Settlement	4	0.02
Common leopard	Natural forest	22	0.25
	Modified	22	0.39
	Settlement	2	0.04
Jungle cat	Natural forest	1	NA
	Modified	24	0.14
	Settlement	4	0.04
Leopard cat	Natural forest	25	0.08
	Modified	10	0.07
	Settlement	07	0.20
Himalayan palm civet	Natural forest	22	0.43
	Modified	18	0.13
	Settlement	2	0.13
Red fox	Natural forest	20	0.11
	Modified	10	0.10
	Settlement	0	NA
Yellow-throated marten	Natural forest	15	0.63
	Modified	4	0.45
	Settlement	2	0.51
Indian crested porcupine	Natural forest	98	0.05
	Modified	122	0.12
	Settlement	16	0.07

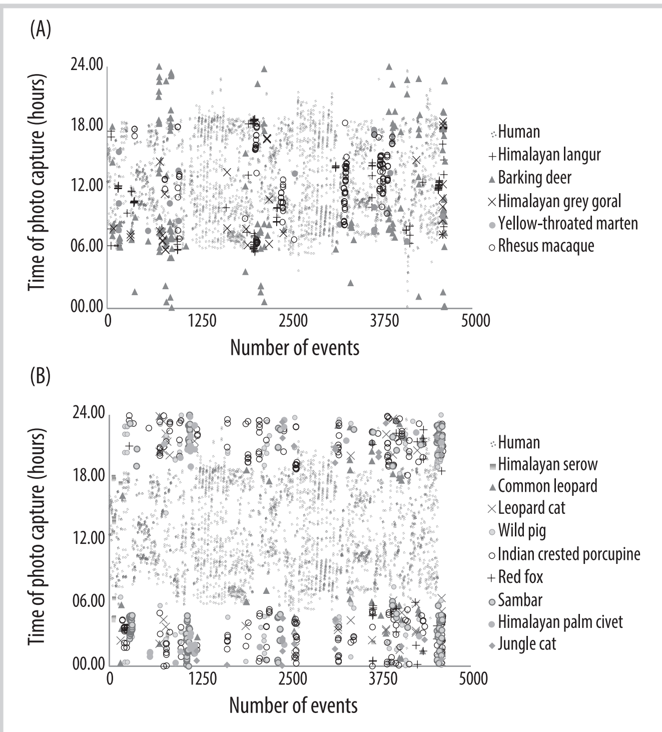
NA, not applicable.

Discussion

Our results show that the majority of species used modified areas, but with some adjustments in usage in space and time. Herbivores such as barking deer, goral, serow, and sambar avoided areas near settlements, as evident from zero to very low captures in such areas. Species such as goral and serow did not use areas that had been modified, such as agricultural lands. This was in accordance with other studies that found these animals were sensitive to human-mediated disturbances, such as trails used frequently by humans (eg tourist trails; Bhattacharya et al 2012), and to agricultural/modified areas and settlements (Paudel and Kindlmann 2012). Species such as barking deer and wild pig have been reported to avoid areas near settlements (Azlan 2006; Paudel and Kindlmann 2012).

Small mammals used almost all habitat types; however, species such as jungle cat, red fox, and civet showed high

FIGURE 5 Temporal patterns of humans and wildlife based on camera trap photo captures in the study area: (A) diurnal species; (B) nocturnal species.



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capture rates in crop fields. This could be because of their diet and/or the type of habitat they prefer (Mudappa 2013). For example, rodents are major pests in crop fields (Stenseth et al 2003), and they are prey for many of the small carnivores, which are consequently attracted to these habitats. Indian crested porcupine was the most common wild animal using all the habitats in study area; being nocturnal, it could directly avoid humans. Studies done elsewhere found similar results for small carnivores, which in general are omnivorous (Fedriani et al 2001; Fuller et al 2010; Rodewald and Gehrt 2014). They are also reported to be tolerant of human-mediated disturbance (Doncaster and Macdonald 1991; Tigas et al 2002). Small and large carnivore species such as red fox (Gloor 2002; Contesse et al 2004; Ditchkoff et al 2006; Baker 2007; Díaz-Ruiz et al 2016; Ghoshal et al 2016), coyotes (*Canis latrans*) (McClure et al 1995; Fedriani et al 2001), spotted hyena (*Crocuta crocuta*) (Abay et al 2011), golden jackal (Macdonald 1979; Yom-Tov et al 1995), and Australian dingo (*Canis lupus dingo*) (Newsome et al 2014) have all been found to be dependent on anthropogenic subsidies in semirural to urban landscapes, shifting their activity to become primarily nocturnal in response to humans.

The large carnivore, common leopard, used fallow and mosaic land more than other natural and nonnatural habitats. The use of shrub-dominated areas by leopards was also found by Aggrawal et al (2011) and Bhattacharjee (2006). This could be due to the cover that this vegetation offers, which is particularly important where chances of human encounters are higher, as is the case in the modified areas. Golden jackal, which was fairly common in these areas in the early 1990s (S Sathyakumar, personal observation), is clearly in decline. This was also reported by people in the study area and is evident from the low number of photo captures. This may be due to an increase in the population of dogs in the human-dominated landscapes. The decline in populations of jackal has been observed in other areas and is a concern for this "once common" species (Pillay et al 2011; Srivastava 2019).

With humans present throughout the study area, it is almost impossible for wildlife to avoid humans spatially, and so we looked at how they negotiated humans temporally. Most of the diurnal species did not show much difference in temporal activity pattern, as was expected. According to Gaynor et al (2018), in order to use anthropogenic areas, wild animals shift to a nocturnal activity. In our study, we found that only a few species reported to have diurnal activity pattern in natural areas or PAs, such as wild pig (Azlan 2006; Grassman et al 2006) and common leopard (Ngoprasert et al 2007; Odden et al 2014; Carter et al 2015; Van Cleave et al 2018), were found to be predominantly nocturnal throughout the study area, including inside forests. However, other diurnal species, such as barking deer, were found to be active also in the night hours; this has not been reported in other studies examining human presence in a landscape, such as those by Griffiths and Schaik (1993), Carter et al (2015), and Ota et al (2019).

The activity of wild pig in modified areas was clumped within a short range of time. Similar patterns were mentioned in Prater (1965). A narrow range of temporal activity was also observed in leopard cat, where the peak activity period in modified areas was from 00:00 h to 03:00 h. Yellow-throated martens were active during daytime, while they followed a more crepuscular pattern in the forest. To the best of our knowledge, this study is the first to describe the time activity for this species. Large carnivores such as tigers (*Panthera tigris*) (Carter et al 2012) and leopards (Ngoprasert et al 2007; Odden et al 2014) have been found to shift their diurnal activity pattern to nocturnal while using human-dominated areas (Azlan and Sharma 2006), as found in our study. Leopards in our study area were predominately nocturnal.

In a previous study, moose (*Alces alces*), a large-bodied ungulate, was found to alter its temporal activity in modified areas, using the area only at night (Bjørneraas et al 2011). A similar large herbivore in our study, the sambar, exhibited nocturnal activity; however, this animal generally follows nocturnal or crepuscular activity in undisturbed areas (Matsubayashi et al 2007). Diurnal species such as barking deer, goral, and marten showed no significant difference in temporal activity pattern between natural and modified areas and in relation to humans. This suggests adaptation to human presence, adopting a strategy of flight if humans are encountered, rather than shifting temporal activity. Sightings of barking deer, followed by goral, were the most common sightings during the present study period. In all these encounters, barking deer ran off into the woods within seconds. This suggests that these animals are habituated to human presence, as also reported by Griffiths and Schaik (1993). We also found that, although a few species had different activity patterns in natural or modified areas, others had similar temporal overlaps with humans in natural and other habitat types, indicating behavioral adaptations allowing animals to survive in human-dominated landscapes. Hence, it seems that adjustment of spatial and temporal patterns of habitat use helps wild animals to utilize modified areas for different purposes. Availability of subsidized food resources (crops for herbivores [Bayani et al 2016; Thinley et al 2017] and rodents/livestock for carnivores [Sekhar 1998; Madhusudan 2003; Rajaratnam et al 2007]), allowing optimal foraging, and cover (use of habitats such as mosaic and secondary scrubland in the study area) seem to govern the use of human-modified area by wild animals. However, long-term studies are required to support our findings and establish the ultimate causes of such patterns of habitat use.

The results of this study highlight that the wild mammals exhibit significant plasticity, allowing them to thrive in human-dominated landscapes. However, co-occurrence of wildlife and humans is often negative (Yom-Tov et al 1995; Baker 2007; Oro et al 2013), involving, for example, crop raiding (Madhusudan 2003; Charoo et al 2011), livestock depredation (Naha et al 2018), attacks on humans (Dhanwatey et al 2013; Naha et al 2019), and retaliatory killings by humans (Mishra et al 2003; Kissui 2008; Pandey 2019). In our study, despite having high overlap with humans, coexistence seemed to be largely positive (personal observation). This is likely to continue as long as the status quo is maintained, but the factors that could cause a tipping point/threshold and the time table over which this might occur can only be understood by long-term observation.

This approach of investigating wild-animal use of human-modified systems outside of PAs has never been carried out in the Indian Himalayan region, making this study important from a conservation point of view. In addition, with the current trajectory of development goals in the Indian Himalaya, such as hydropower plants (Grumbine and Pandit

2013) and urbanization (Pandit et al 2014), this is a critical time to study how mountain ecosystems can be developed sustainably. Our study demonstrates a new design for estimating habitat use by mammals in a heterogeneous area of human-modified landscapes in mountain systems. Since mountain ecosystems are similar all over the world (Smith 2014), with terrace farming and villages interspersed with forests (Heimbuch 2020), our study has wider implications.

Our findings are preliminary and showcase how animals adapt to live in human-dominated areas, but they also show that certain species, especially herbivores, can be negatively affected by modifications of natural habitats. Although we suggest that development activities should be carried out in a sustainable way, further studies investigating the extent to which different species are affected by various land-use types are required to provide better insights.

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Supplemental material

APPENDIX S1 Criteria used to categorize habitat types described in the study area.
APPENDIX S2 Supervised classification accuracy assessment report.
APPENDIX S3 Unsupervised classification accuracy assessment report.

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