RESEARCH ARTICLE

Coexistence in multi-use landscape: linking human activities with functional traits of wild mammals in southern India

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Abstract

Context Human presence and land-use activities influence habitat use and activity of species. It is crucial to study the ecological and anthropogenic determinants that drive these relationships.

Objectives We investigated the effects of land-use change and human presence on the habitat use of seven mammalian species and on their activity patterns.

Methods We conducted a camera-trapping survey in Ballari district, India. We deployed camera-traps at 1457 sampling grid cells across Protected Areas (PAs), Reserved Forests (RFs), and adjoining fringe mosaic farmlands (FMFLs). We assessed the influence of 19 covariates related to habitat features, landscape-level human presence, climate, and local-level human presence on species habitat use. We examined the diel activity patterns and activity levels of mammals within different land-use types.

Results Four species exhibited a net negative response to increasing human presence, while three species exhibited positive responses. Respectively, proximity to farmlands, and settlements positively influenced habitat use by *Panthera pardus*, and *Lepus nigricollis*,. Increasing direct human presence negatively affected *Sus scrofa* habitat use. Large body-sized species exhibited higher diurnal activity in PA/

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RF compared to FMFL while smaller-sized (≤ 2.2 kg) species maintained similar activity patterns across land-use types. Generalist meso-predators exhibited more diurnal activity in RF/FMFL.

Conclusions Ecological and life history traits were strong predictors of species responses to increasing human presence which favoured smaller and generalist species. These insights into the complex mechanisms through which human activities shape mammal communities are important landscape level perspectives on conservation.

Keywords Activity · Camera trapping · Farmland · Habitat use · Human presence · Protected area

Introduction

Land use change and increased human activities are the prominent drivers of ongoing biodiversity loss (Powers and Jetz 2019; Suraci et al. 2021). These forces have a strong impact on the distribution of mammalian species (Polaina et al. 2019; Ramesh and Downs 2015) and underlie the declining population size of many mammals (Baisero et al. 2020; Rondinini and Visconti 2015). The ability of wild mammals to coexist with human in human-dominated landscapes may be strongly influenced by a species, ecological and life history traits (Gascon et al. 1999; Samia et al. 2015; Suraci et al. 2021). The resulting differential responses of species to human disturbance have a filtering effect at the community level, favoring species that can adapt to modified landscapes (Bellón et al. 2022; Drouilly et al. 2018; Ehlers Smith et al. 2018; Penjor et al. 2021). Consequently, human disturbance reshapes mammal communities in a way that can be predicted from suites of species traits (Estes et al. 2011; Schmitz et al. 2018). Therefore, understanding the effects of human-induced modifications on wild mammals has become a key aspect in biodiversity conservation at many scales ranging from local to global.

Species survival and success in disturbed and modified landscapes are heavily influenced by their ecological and life history traits (Galán-Acedo et al. 2019; Parsons et al. 2018). These traits interact with multiple anthropogenic stressors changing species behavior and distribution (Doherty et al. 2021; Nickel et al. 2020). Specifically, human presence can induce

fear responses that alter habitat use and suppress activity (Gaynor et al. 2018; Oberosler et al. 2017). Such changes are often influenced by body size, home range size and trophic position (Clinchy et al. 2016; Suraci et al. 2021). Species with large home ranges are most vulnerable to habitat loss due to land conversion (Crooks et al. 2017; Milda et al. 2023a; Ripple et al. 2014). Carnivores are particularly sensitive to human activity and habitat alteration (Di Minin et al. 2016; Milda et al. 2023a). In contrast, species that habituate to the disturbance of human activity and exploiting anthropogenic food subsidies can thrive in human modified areas (Athreya and Karanth 2016; Wang et al. 2015). Species with traits like wide habitat type tolerance, nocturnal activity, and higher dietary flexibility can more easily adapt to modified landscapes (Larson et al. 2015; Newsome and Van Eeden 2017; Šálek et al. 2015). Furthermore, prey species and meso-carnivores can benefit when human presence reduces local predation pressure (Crooks 2002; Ordenana et al. 2010). Thus, understanding how functional traits of wild mammals influence their response to human disturbance can provide insights for conservation planning.

The importance of conserving biodiversity by creating Protected Areas (PAs) has been recognized by authorities around the globe (Dudley 2008; Hockings 2003). In India, PAs are wildlife sanctuaries that fall into IUCN category IV and include a very high degree of protection from poaching, grazing, and Non-timber Forest Product (NTFP) collection (Badola 1999; Ghosh-Harihar et al. 2019). However, PAs only encompass a small proportion of the landscape, less than 5% of the total landmass (Ghosh-Harihar et al. 2019). Consequently, PAs are only efficient in safeguarding a small proportion of diversity, as majority of species persist outside PAs (Schmitt et al. 2009). The non-protected forested areas in India are recognized as Reserved Forests, Community Reserves, and unclassed forests (Macura et al. 2011). Reserved forests (RFs), owned by state governments, cover 13.2% of India's landmass and often contribute to buffers and corridors for PAs (Ghosh-Harihar et al. 2019; Shahabuddin and Thadani 2018). RFs have weaker safeguards against wildlife harvesting and livestock grazing by local people compared to PAs (Milda et al. 2020). Natural resource extraction is allowed in many RFs, putting additional pressure on these landscapes (Forest Survey of India 2019).

The degradation of wildlife habitats (PAs and RFs), together with the increasing expansion of agricultural land, has a strong negative impact on biodiversity. Many mammalian species thrive in farmlands and forest remnants outside of PAs and RFs (Schmitt et al. 2009), which we will refer to as Fringe Mosaic Farmlands (FMFLs) in this study. FMFLs represents the anthropogenic land-use mosaic of agricultural lands. Thus, FMFLs are prone to more human disturbances and has lower habitat heterogeneity than PAs or RFs. Assessing anthropogenic landscape variables related to land-use types within the multi-use landscape mosaic and their impact on species distribution and behaviour at different scales and time frames is critical for biodiversity conservation (Noon et al. 2012; Roland et al. 2013; McDonald et al. 2015).

The need for research investigating factors shaping diverse mammalian community assemblages in less studied parts of the world is great (Pardikar 2020; Rowan et al. 2020). The landscape of the Ballari district situated in the Deccan plateau of India is one of such less studied area which has undergone extensive land-use change during the last century. Specifically, mining activities within forested habitats including more traffic from heavy vehicles have increased (Intercultural Resources 2014). Encroachment into forests from agrarian activities by locals, including heavy overgrazing, and collection of Non-timber Forest Product (NTFP) collection, as well as poaching have increased (Behera et al. 2022; Meena 2013; Rudramuniyappa 1997). All these activities exert intense pressure on the remnant forest patches

contributing to the decline of many mammalian species. These activities also increase the frequency of negative human-wildlife interactions in the form of livestock predation, human injury or death, wild animal mortality, and crop damage (Martins-Oliveira et al. 2021; Meena 2013; Sharp et al. 2020). Resolving increasing anthropogenic pressure and the associated decline of mammalian species in such disturbed ecosystems requires broad landscape-level studies. Such studies can help discern the primary determinants of species extinction at the local level and identify solutions to help forest managers ensure effective wildlife conservation (Jones 2011). We address a critical knowledge gap regarding the influence of anthropogenic and ecological factors on specific species in our study system to understand forces shaping the mammalian assemblage.

We examined the effect of anthropogenic disturbances on seven mammal species found within Ballari district using landscape-scale variables from four broad categories (habitat features, landscape-level human presence, climate, and local-level human presence). We report habitat use of black napped hare (*Lepus nigricollis*), golden jackal (*Canis aureus*), Indian fox (*Vulpes bengalensis*), jungle cat (*Felis chaus*), leopard (*Panthera pardus*), sloth bear (*Melursus ursinus*) and wild pig (*Sus scrofa*). This group of species includes varied functional traits like body sizes, diets, trophic positions, and home range sizes. All of these species are native to the study site and details about their functional traits (Table 1) and IUCN red list statuses are provided in Supplementary

Table 1 List of study species with their important functional traits and the number of independent photographs across land-use types

Sl. No.	Species	Functional traits (Body-size - Home range - Diet - Activity)	No. of individual photographs across land-use types		
			Protected Areas	Reserved Forests	Fringe Mosaic Farmlands
1	Black-naped hare	Small- Small- Herbivore- Crepuscular/Nocturnal	972	2272	1111
2	Golden jackal	Small- Small- Omnivore- Nocturnal	125	491	203
3	Indian fox	Small- Small- Omnivore- Crepuscular/Nocturnal	77	402	146
4	Jungle cat	Small- Small- Carnivore- Typically diurnal	59	238	264
5	Leopard	Large- Large- Carnivore- Nocturnal	54	245	109
6	Sloth bear	Large- Medium- Omnivore- Mostly nocturnal	95	151	206
7	Wild pig	Large- Medium- Mostly herbivore- Diurnal	236	466	696

Body size (Small/Large); **Home range** (Small/Medium/Large); **Diet** (Herbivore/Omnivore/Carnivore); **Activity** (Diurnal/Crepuscular/ Nocturnal). Based on Menon 2023

Table S1. Our main objective was to understand how the combination of a species' functional traits influences its response to human activities. Specifically, we predicted that species with; larger body sizes, larger home range sizes, specialized diets and top carnivores, will be negatively affected by variables associated with landscape-level or local level human presence (Ripple et al. 2014). We predicted that habitat use, and activity of small and generalist carnivores will respond positively to increased human presence and availability of farmlands (Katna et al. 2022) and that the hare habitat use will be positively associated with PA. We predicted that habitat use by large mammals would be positively associated with natural habitat with dense canopy coverage (Andrade-Núñez and Aide 2010). We also compared activity patterns and activity levels between the study species across three land-use types. We predicted that mammalian species sensitive to human activities would exhibit highest nocturnal activity in FMFL, followed by RFs and PAs. We also predicted an increase in the concentration of activity i.e., a shorter activity window in disturbed land use types (FMFL and RF).

Methods

Study area

We conducted our study within the jurisdictional area of the Ballari territorial forest division that forms a part of the Deccan Peninsula of India (between 14° 30′ and 15° 50′ north latitude and 75° 40′ and 77° 11′ east longitude; Fig. 1). The region lies between 550 and 750 m AMSL with the terrain varying from open plains to undulating areas with some patches of rugged hills (Meena 2013). The average annual temperature varies from 20 to 40 °C. Our study area consists of a mostly dry landscape with an average annual rainfall of around 574.9 mm. The central part of the district contains tropical dry deciduous forests predominately composed of species like *Albizzia amara, Chloroxylon swietenia, Hardwickia binata, Grewia tiliaefolia*, and *Azadirachta indica*). The other forested patches represent dry thorn forests with sparse vegetation (Champion and Seth 1968), that are dominated by *Albizzia amara, Acacia catechu, Cassia auriculata, Euphorbia spp.*, and *Zizyphus spp.*).

Ballari is one of the most economically vulnerable districts in the country and its economy is primarily based on mining and agrarian activities. The local people maintain large cattle populations for sustenance/economic prosperity and are highly dependent on NTFP collection. The district contains rich deposits of minerals of economic importance like iron and manganese (Meena 2013). More than 5000 ha of land within the study area is actively mined, with most of the mines situated within RFs.

Data collection and analyses

Camera trapping data were collected within the forested areas of Ballari district including PAs [Daroji (est. 1994) and Gudekote (est. 2013) Sloth bear sanctuaries], RFs, and FMFL (a 1 km buffer surrounding forest boundaries). We established a camera trapping grid composed of 1 km^2 cells as sampling units by overlaying a 1×1 km^2 grid across the study areas using ArcGIS 10.1 (ESRI, Redlands, CA, USA). We used a land cover layer that we obtained from Karnataka Forest Department to identify the land cover types in the study area.

We conducted camera-trapping surveys to to collect occurrence data during a period of 21 months between January 2019 and October 2021. Within each 1 km^2 grid cell, we walked for at least 1 km around the centroid of the grid cell and identifed the best potential camera sites based on mammalian sign evidences (sightings, scats/pellets, and tracks of mammals) (Jhala et al. 2008; Kalle et al. 2013; Karanth and Nichols 2002; Ramesh et al. 2012). We installed a single passive infrared camera trap (Cuddeback digital 20MP Blue Series, USA) at each sample site within each grid cell. Camera traps were fitted 30 cm above the ground level and placed along dirt roads, animal trails, rivers, and stream beds, near water holes, etc. that are commonly used by study species. We maintained a minimum distance of approximately 500 m between any two cameras to insure spatial independence of our samples. In total, we sampled 1457 grid cells including 251 grid cells within PAs, 756 grid cells within RFs, and 450 grid cells within FMFL. The number of sampling sites per land-use type was proportional to to the occurrence of those land-use types within in the study area. We deployed 142–145 camera traps simultaneously and shifted those cameras to other grid cells throughout
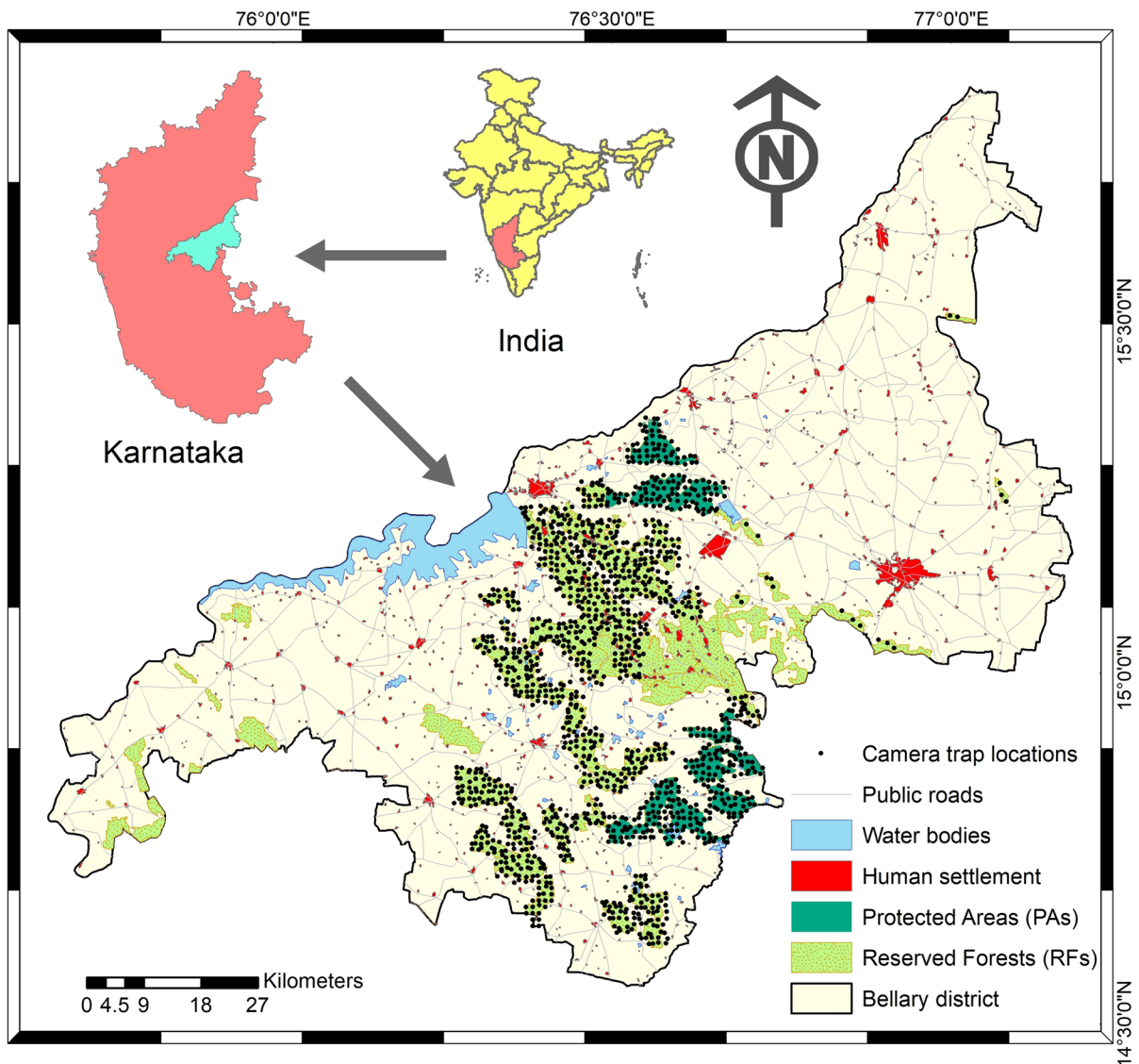
Fig. 1 Camera trap locations of the survey area in Ballari district, Karnataka, across Protected Areas (PAs; *n*=251), Reserved Forests (RFs; *n*=756) and the adjoining fringe mosaic farmlands (FMFLs; *n*=450). Camera traps located in farmlands i.e., outside forested landscape (PAs/RFs; within 1 km from forest boundaries) are the traps located in FMFLs.

the study period. We set camera traps (30s motion triggered delay setting) to run continuously for 22 days within each grid cell and collected data weekly. In each camera trap location, we visually estimated the percentage of canopy coverage, tree density, percentage of rockiness, and shrub coverage within a circular plot with a radius of 20 m (Table 2). After retrieving photos from the camera traps, we measured local-level human presence at each site using four proxies: relative abundance index (RAI) of human

(on foot or in vehicles), cattle, goats-sheep, and domestic dogs. We calculated RAI of a species as the total number of independent (one photograph with 30 min intervals) photographs of that species divided by the total number of camera trap-nights at that location (Palmer et al. 2018; O'Brien et al. 2003). We estimated proximity variables like proximity to road, settlements, farmlands, etc. using verified spatial layers like GRIP global roads database, and Roy et al. 2015 (after converting these rasters into shapefiles)

Table 2 List of 21 predictor variables classified under four broad categories that are used in analysis

Sl.	Group	Covariates	Description	Type	Models [Occupancy(O) / Detection(D)]	Abbreviation	Source of extraction
1	Habitat features	Elevation / Altitude	Elevation of the camera site	Continuous	O	Elevation	ArcGIS Online – DEM of Asia (Spatial resolution: 1 km)
2		Water body	Proximity to the nearest water body	Continuous	O, D	Waterbody	Vegetation type map (Roy et al. 2015; spatial resolution: 60 m)
3		Canopy coverage	Percentage of canopy coverage in the 20 m radius around sampling sites	Continuous	O	Canopy	Field data collection
4		Rockiness	Rocky coverage of the 20 m radius around sampling sites	Continuous	O	Rockiness	Field data collection
5		Tree density	Number of trees in the 20 m radius around sampling sites	Continuous	O	Tree	Field data collection
6		Shrub coverage	Percentage coverage of shrub in the 5 m radius around sampling site	Continuous	O, D	Shrub	Field data collection
7		Terrain type	Type of terrain Undulating or Plain	Categorical	O	Terrain	Field data collection
8		Proximity to farmland	Proximity to the near agricultural land	Continuous	O, D	Farmdist	Vegetation type map (Roy et al. 2015)
9		Proximity to scrub forest	Proximity to the nearest extent of scrub forest	Continuous	O	Scrubdist	Vegetation type map (Roy et al. 2015)
10		Proximity to deciduous forest	Proximity to the nearest extent of deciduous forest (both dry and moist deciduous)	Continuous	O	Decidist	Vegetation type map (Roy et al. 2015)

Table 2 (continued)

Sl.	Group	Covariates	Description	Type	Models [Occupancy(O) / Detection(D)]	Abbreviation	Source of extraction
11	Landscape-level human presence	Proximity to road	Proximity to the nearest public road (Including mining roads)	Continuous	O, D	Road	GRIP global roads database (Spatial resolution: 8 km), modified using Google Earth and field observation
12		Proximity to human settlement	Proximity to nearest human settlement (Village, town, or mine)	Continuous	O, D	Settlement	Vegetation type map (Roy et al. 2015)
13		Protected Areas (PAs)	Camera sites located in PAs	Categorical	O	PA	Land-cover map obtained from Karnataka Forest Department (Spatial resolution: 60 m)
14		Reserved Forests (RFs)	Camera sites located in RFs	Categorical	O	RF	Land-cover map obtained from Karnataka Forest Department
15		Adjoining fringe mosaic farmland (FMFL)	Camera sites located in mosaic farmlands	Categorical	O	FMFL	Land-cover map obtained from Karnataka Forest Department
16	Climate	Precipitation (in mm)	Mean annual precipitation	Continuous	O	Preci	Bioclim layer obtained from Worldclim (Spatial resolution: 1 km) https://www.worldclim.org/
17		Season	Type of season 1) Wet 2) Dry	Categorical	O, D	Season	weatherspark.com
18	Local-level human presence	RAI Human	Human relative abundance index	Continuous	O, D	Human	Camera trap data
19		RAI Cattle	Cattle relative abundance index	Continuous	O, D	Cattle	Camera trap data
20		RAI Goat-Sheep	Goat and Sheep relative abundance index	Continuous	O, D	Goatsheep	Camera trap data
21		RAI Dog	Dog relative abundance index	Continuous	O, D	Dog	Camera trap data

and the Euclidean distance tool in ArcMap 10.3 (Arc-Map 10.3, Software. Redlands, CA: Esri Inc, 2016). Details for the covariates are provided in Table 2.

Habitat use and detection probability

We considered 21 predictor variables estimated from camera sites to be important to the study species. We categorised these variables into- (1) Habitat features, comprising naturally occurring features or habitat characteristics; (2) Landscape-level human presence, comprising features associated with varying degrees of human footprint and landscape management; (3) Climate, comprising two climatic features and (4) Local-level human presence, comprising the RAI of humans, dogs, and livestock at camera stations (Table-2).

Considering the average home range size of the study species [hare: 0.01–0.02 km^2 (Kirk and Bathe 1994), jackal: 3.1–23.7 km^2 (Katna et al. 2022), fox: 1.16–10.71 km^2 (Katna et al. 2022), jungle cat: 1.01–26.48 km^2 (Katna et al. 2022), leopard: 8–65 km^2 (Odden et al. 2014), bear: 12–85 km^2 (Yoganand et al. 2005), and wild pig: 0.62–48.3 km^2 (Garza et al. 2018), we interpreted occupancy estimates as habitat use because the home ranges of some of our study species are larger than the grid cell size used. This interpretation of our results as probability of habitat use, and not probability of occupancy at each sampling unit is done to in part minimize the impact of our likely violating the assumption of closure (Burton et al. 2015). We treated each camera site as an independent sample and sampling occasion as a temporal repeat of the survey. In our analyses, we assumed the habitat use of a species to be independent of other species. We developed '0'-'1'matrices for each species. Rows represented sample locations and columns daily sampling occasions. Detection and non-detection during successive sampling occasion were respectively indicated with '1' and '0' in this matrixd (Otis et al. 1978). We used a single-season occupancy model to estimate site occupancy/habitat use (Ψ) and detection probability (*p*) of study species (MacKenzie et al. 2017) using the package "unmarked" (Fiske and Chandler 2011) in program R (R Core Team 2020). Prior to modeling, we standardized all continuous site covariates to z-scores which allows model coefficients to be interpreted as the change in the log-odds ratio of habitat use relative to a 1-standard deviation change

in a covariate from its mean (Cooch and White 2005). To avoid multi-collinearity problems, we tested the correlations among independent variables (Graham 2003) using Pearson's correlation coefficient (Supplementary Figure S1) using the package "corrplot" in program R and didn't use highly correlated variables (r > 0.60) in the same model (Wei and Simko 2021). We removed a few highly correlated independent variables (decidist: proximity to deciduous forests and FMFL: fringe mosaic farmlands) before modelling. Details on the selection of relevant variables to estimate habitat use and detection probability in our models are provided on Table 2. We followed stepwise model selection procedures and the goodness of fit for model selection as described in Burnham and Anderson (2002) and ranked the models using AIC (Akaike information criterion). We considered the models with the lowest AIC values (ΔAIC $\leq$ 2) as the best descriptors of species habitat use and detection probability among candidate models (Burnham and Anderson 2002).

Activity patterns and activity levels

We investigated the diel activity patterns for the seven study species across three land-use types. The activity patterns of a species are the temporal data that provide information on the diel trends of its actions (Gerber et al. 2012). Studying activity patterns provides insight into the ecological processes that shape the space use by an animal community (Houngbégnon et al. 2020). We subsampled the detection data considering consecutive detections within a 30 min interval as a single event (Meek et al. 2014; Zimmermann et al. 2016). We segregated all independent events of a species into three categories for activity pattern analysis based on land use type (Table 1). Then we performed pairwise comparisons of activity patterns of species between all three land use types (PA vs. RF, RF vs. FMFL, and FMFL vs. PA) by estimating the overlap coefficient Δ (ranging from 0 to 1 i.e., no overlap to complete overlap) and its confidence interval (Ridout and Linkie 2009). We performed statistical analyses and produced Kernel density estimation curves using the 'Overlap' package (Meredith and Ridout 2016) in Program R 4.0.5 (R Core Team 2020). Kernel density estimation is a non-parametric method for estimating the probability density function of a distribution of records (Linkie and Ridout

2011). Activity level of a species is the proportion of time that species spend being active during an entire day (Rowcliffe et al. 2014). This method assumes that all individuals in the sampled population are active at the peak of the daily activity cycle. We used the function compareAct() in the package "Activity" Program R 4.0.5 (R Core Team 2020) to conduct Wald test for the statistical difference between two or more activity level estimates. We quantified the activity level estimates of study species in the different land-use types.

Results

Camera trapping survey at 1457 sampling sites, $n = 31{,}702$ trap-nights yielded photographs of 24 wild mammalian species, livestock, dogs, and humans (Supplementary Table S1). We conducted occupancy analysis for seven wild mammalian species that are widely distributed across our study site and, for which we had sufficient data for occupancy analysis (MacKenzie et al. 2017). We didn't include some species for analysis as they occurred in low densities (Neilson et al. 2018). Hare had the highest naïve occupancy 0.528, followed by wild pig = 0.318, jungle cat = 0.217, jackal = 0.203, fox = 0.189, leopard = 0.173, and bear = 0.15. We determined the best-fit models for each species and their log-transformed

parameter estimates of habitat use Ψ and detection probabilities p with detailed results listed in Table 3; Fig. 3, respectively. The summary of AIC model selection and parameter estimates of habitat use and detection for study species are listed in supplementary tables S2-S8. The number of variables influencing patterns of habitat use and detection probability in well-supported models ($\Delta AIC \le 2$), ranged from 4 to 8 across the study species (Table 3). Estimates of habitat use Ψ with standard errors varied from 0.239 ± 0.023 to 0.538 ± 0.028 across study species and models (Fig. 2). Hares had the highest estimates for habitat use. Wild pigs had the second highest habitat use after hares (Fig. 2). Jackals, foxes, and sloth bears had lower habitat use compared to other study species (Fig. 2). Hares had the highest detection probability, followed by jackals and foxes (Fig. 2). The residuals of the top models for jackal, fox, jungle cat, and hare did not exhibit any spatial autocorrelation [Moran's I for jackal = 0.0006 ($P = 0.38$); fox = -0.0026 ($P = 0.82$); jungle cat = 0.0009 ($P = 0.17$); and hare = -0.0007 ($P = 0.84$)]. However, top model residuals for leopard, bear, and wild pig documented some spatial autocorrelation [Moran's I for leopard = 0.0066 ($P = 0.00$); bear = 0.0108 ($P = 0.00$); and pig = 0.0022 ($P = 0.03$)].

We found that variables related to human presence whether at landscape level or local level, were
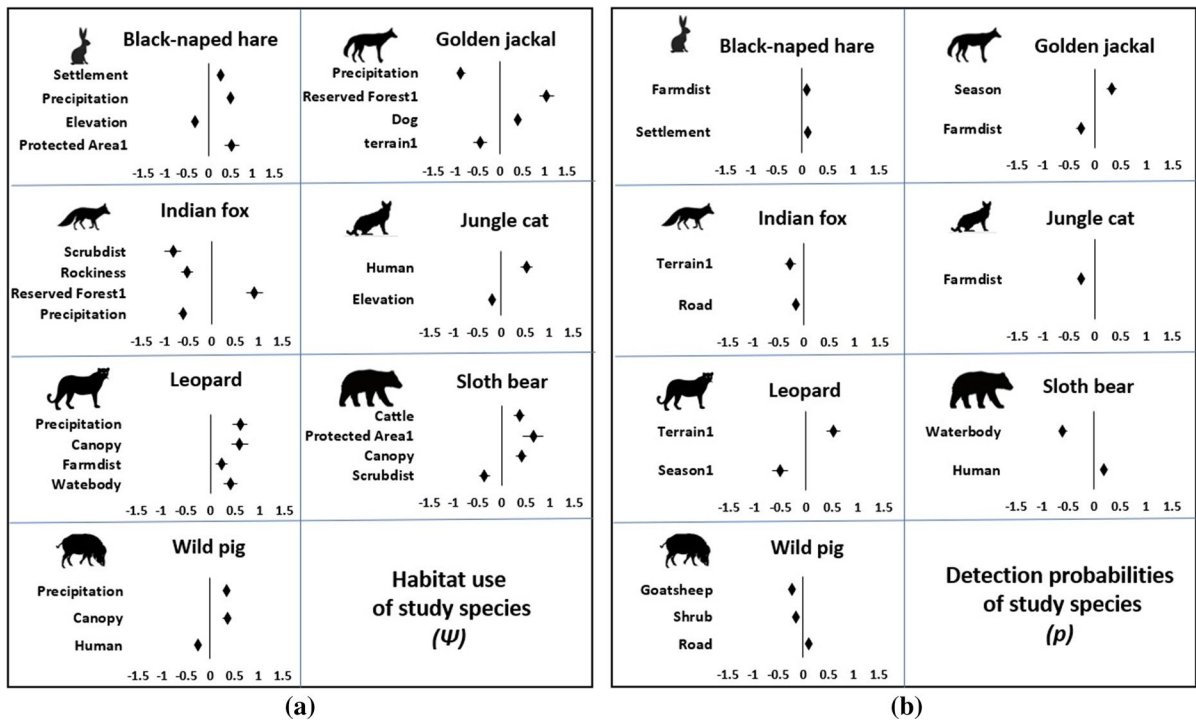
Fig. 2 Habitat use and detection probabilities of study species present in Ballari district, India
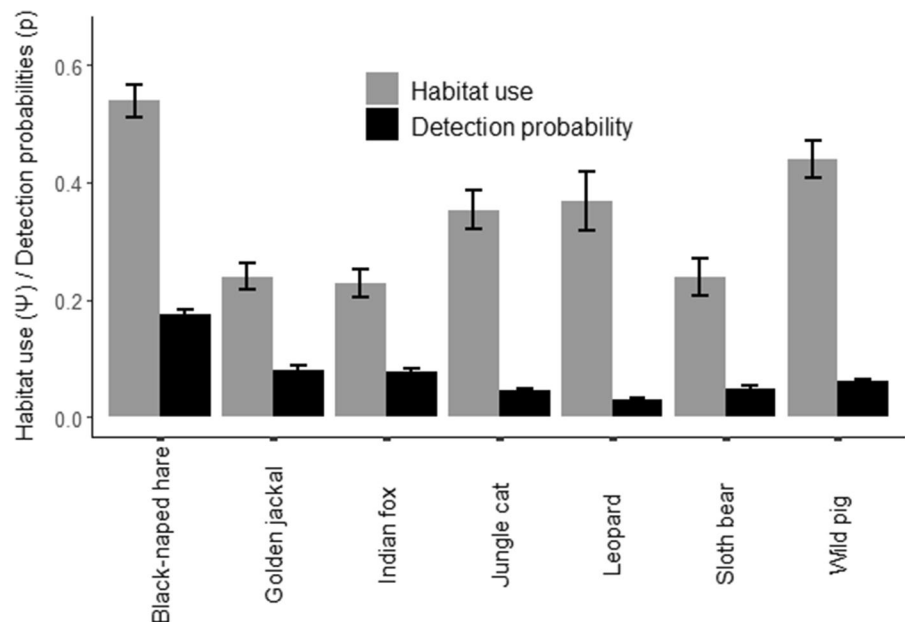
Table 3 Best-fit logistic models based on the Akaike Information Criterion scores for predicting the occupancy (habitat use) and detection probability of seven mammal species in the study area

Species	Best-fit Model(s)	AIC	Δ AIC	AIC Weight	No. Par.
Black-naped hare	p (~ farmdist + settlement) Ψ (~ settlement + preci + elevation + PA)	18003.80	0.00	0.79	8
Golden jackal	p (~ season + farmdist) Ψ (~ preci + RF + dog + terrain)	5635.16	0.00	0.90	8
Indian fox	p (~ terrain + road) Ψ (~ scrubdist + rockiness + RF + preci)	4899.16	0.00	0.71	8
Jungle cat	p (~ farmdist) Ψ (~ human + elevation)	4913.51	0.00	0.79	5
Leopard	p (~ terrain + season) Ψ (~ preci + canopy + farmdist + waterbody)	3700.81	0.00	0.74	7
Sloth bear	p (~ waterbody + human) Ψ (~ cattle + PA + canopy + scrubdist)	3722.90	0.00	0.75	8
Wild pig	p (~ goatsheep + shrub + road) Ψ (~ preci + canopy + human)	7375.29	0.00	0.82	8

Abbreviations: We list all models with a Δ Akaike Information Criterion ΔAIC < 2.00, number of parameters No. par., AIC Weight., proximity to agricultural land 'farmdist', proximity to the nearest extent of scrub forest 'scrubdist', elevation at the camera site 'elevation', type of terrain (undulating/plain) 'terrain, rocky coverage of at the camera trapping grid 'rockiness', percentage of canopy coverage at the camera site 'canopy', proximity to the natural water source 'waterbody', proximity to human settlement 'settlement', proximity to the public road 'road', camera sites in PAs "PA", camera sites in RFs 'RF', mean annual precipitation 'preci', type of season (wet/dry) 'season', relative abundance index of human 'human', relative abundance index of cows and buffaloes 'cattle', relative abundance index of goats and sheep 'goatsheep', relative abundance index of free-ranging dogs 'dog'

Fig. 3 Log-transformed parameter estimates for explanatory variables from the top (a) habitat use and (b) detection probability model for mammalian species in Ballari, Karnataka, India

associated with study species habitat use. Proximity measures like distance to human settlement and agricultural farmlands were positively associated with the habitat use of hares and leopards, respectively. Distance to major water bodies was positively associated with the habitat use of leopards. Variables associated with local-level human presence were negatively associated with wild pig habitat use while they were positively

associated with habitat use by jackals and jungle cats. Habitat use of bears and hares was highest in PAs while the habitat use of jackals and foxes was highest in RFs. Unexpectedly, relative cattle abundance emerged as an important predictor for increased habitat use of bears. Canopy coverage and mean annual precipitation were the two common predictors across top models for three and five species, respectively (Fig. 3a and b). The dense canopy coverage positively influenced the habitat use of leopards, bears, and wild pigs. Mean annual precipitation positively influenced the habitat use of hares, leopards, and wild pigs while it had a negative impact on the habitat use of jackals and foxes. The availability of plains positively influenced the habitat use of hares and jungle cats. The most common covariate for detection probability was proximity to the farmlands. Higher detection probabilities for jackals and jungle cats were associated to close proximity to farmlands while this significant trend was reversed for hares.

Activity patterns of species varied across the three land use types (PA vs. RF, RF vs. FMFL, and FMFL vs. PA) (Fig. 4). Activity patterns of all species showed bimodal peaks with first peaks occurred between late evening and midnight while second peaks occurred during early mornings. Hares and jungle cats exhibited similar activity patterns across three land use types. Activity patterns of hares in RF and FMFL were very similar to each other with the mean kernel temporal overlap coefficient estimate of 0.94 (Table 4). Jackals and foxes had higher diurnal activities in RF and FMFL than in PA (Fig. 4; Table 4). While leopards, sloth bears, and wild pigs had higher diurnal activity patterns in wildlife habitats like PA/RF than in FMFL (Fig. 4; Table 4). Activity level estimates of all study species varied across land use types. The activity level of sloth bears and hares in PAs and RFs were significantly higher than in FMFL (Table 5). Leopards, jackals, wild pigs, and hares had significantly higher activity levels in PAs/RFs, relative to FMFL (Table 5). Foxes had significantly higher activity levels in RFs, relative to PAs/FMFLs while there was no significant difference in activity level estimates for jungle cats across land-use types.

Discussion

Intensification of human disturbance has driven local extinction for most mammals during recent centuries

(Wan et al. 2019). Landscape-level studies describing the effects of human disturbance on the distribution of large mammals are essential to understand how to protect their populations from further extinction. Our investigation of habitat uses and activity of seven mammalian species provides a thorough understanding of mammalian responses to anthropogenic disturbances in a highly fragmented landscape. We found that all species' habitat use, and activity patterns are not affected equally by human presence and land use activities. Our landscape-level spatial analysis results confirmed that accelerated anthropogenic activities have more detrimental effect on species with larger body size, larger home range size, higher trophic level, specialist diet, and less nocturnal habit. The results of our analysis of temporal trends of larger mammals showed adjustment in diel activity pattern towards more nocturnality is strongly influenced by increasing human activity and reduction of habitat heterogeneity across land-use types. Some of our study species were highly sensitive to land conversion and reduction of natural habitat while others showed varying tolerance to human-modified habitats. Our findings are consistent with previous studies demonstrating that pristine natural habitats like Protected Areas are the most favourable habitats for large mammals (Pacifici et al. 2020). Thus, our study provided an informative perspective on the decline of several species by identifying the important land use changes that altered their habitat use and behavior within our poorly understudy study area.

In landscapes that are prone to heavy anthropogenic disturbances, it's important to identify how land use changes impact different species (Ramesh and Downs 2015; Sodhi et al. 2010). Ballari district is a landscape that experiences heavy human pressure in form of mining activities, livestock over-grazing, and illegal wildlife harvesting. Our analysis revealed that each study species was distributed throughout the entire study area, but they used land types differently. The difference in the distribution of these species indicates varying levels of tolerance to human disturbances. The two the most widely distributed species within this landscape were hare and wild pig which may be important as these are two major prey species in this system. Leopards, sloth bears, wild pigs, and hares preferred intact undisturbed forests (Ripple et al. 2014). While meso-predators like jackals, foxes, and jungle cats used more modified landscapes, this is

Fig. 4 Comparison of Kernal density activity patterns of focal species in different land use types [Protected Areas (PAs) vs. Reserved Forests (RFs) vs. adjoining fringe mosaic farmlands (FMFL) in Ballari, Karnataka, India
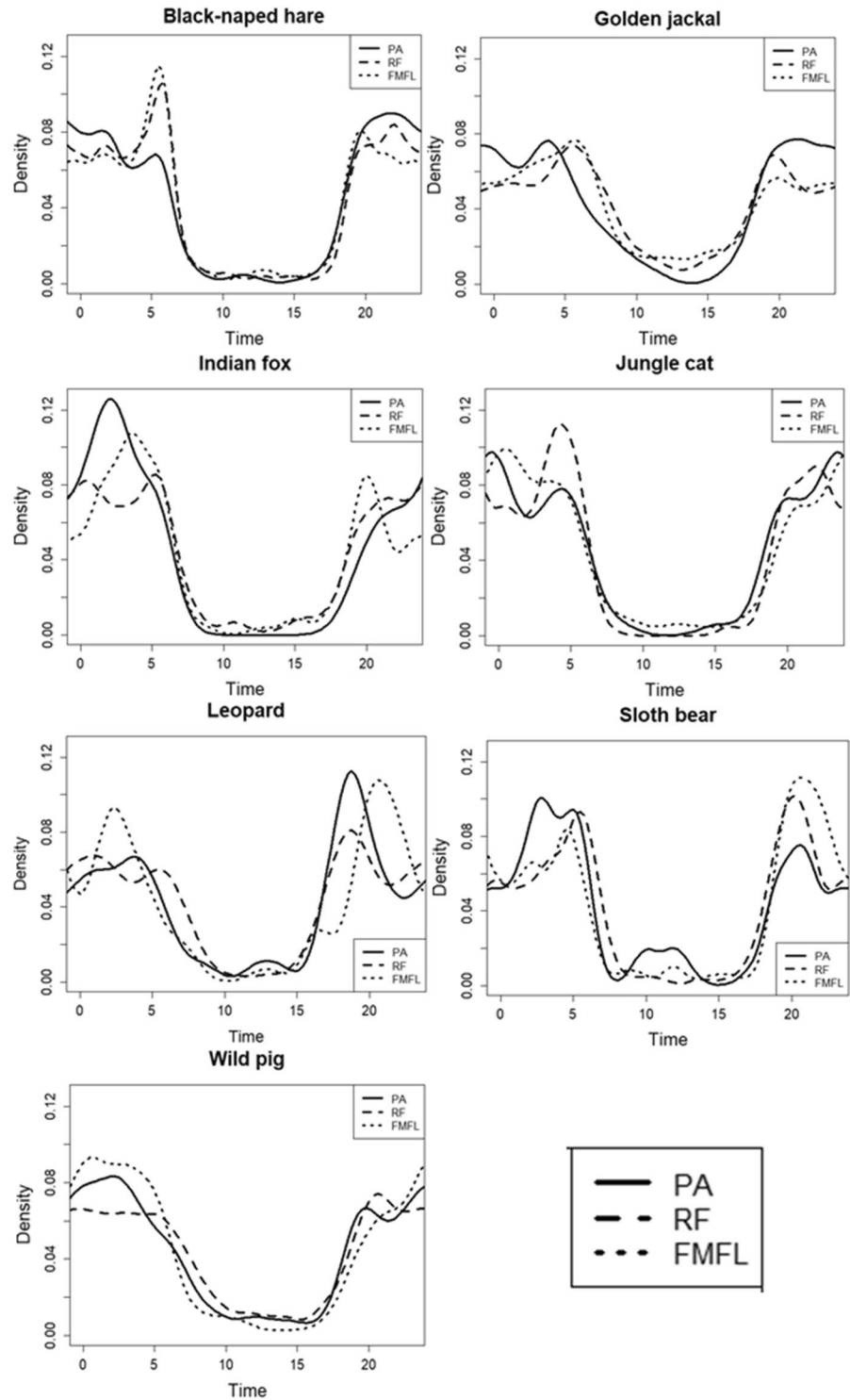
consistent with many prior studies on meso-predators (Beasley et al. 2011; Torre et al. 2022; Zamuda et al. 2022).

Species occurrence can be strongly influenced by the quantity and quality of available habitat (Ceballos and Brown 1995; Ramesh and Downs 2015;

Table 4 Temporal overlap coefficient estimates of study species across land use types (pairwise)

Species	PA vs. RF	RF vs. FMFL	FMFL vs. PA
Black-naped hare	0.90	0.94	0.88
Golden jackal	0.85	0.94	0.85
Indian fox	0.84	0.87	0.83
Jungle cat	0.87	0.85	0.90
Leopard	0.87	0.78	0.79
Sloth bear	0.84	0.87	0.82
Wild pig	0.91	0.85	0.90

Land use types: PA Protected Areas, RF Reserved Forests & FMFL Fringe Mosaic Farmlands

White et al. 1997) and our results supported these findings. Agricultural lands negatively influenced the leopards' habitat use suggesting the importance of natural forested habitats for this species as shown by Gubbi et al. (2020). On the other hand, the abundance of small prey species for meso-carnivores like jackals, foxes and jungle cats is higher in agricultural lands than forest habitats (Alain et al. 2006). High food availability, protection against large predators, and their ability to use human resources undoubtedly all contribute to increased habitat use and detection of these meso-predators within RF and FMFL (Carricondo-Sanchez et al. 2019; Šálek et al. 2014; Vanak and Gompper 2010). The preference of hares for PAs within our study area may be associated with restricted poaching activities within this land use because hares are heavily poached across our study area (Behera et al. 2022). The positive association of hare habitat use with proximity to human settlement supports this hypothesis. Our finding that leopard habitat use was positively associated with proximity to water is likely specific to our study area. Ballari district is a dry landscape and all the major water sources are either situated near human settlement or associated with higher human presence (Meena 2013). Habitat use of sloth bears was higher in PA.

Table 5 Comparison of activity level estimates of seven study species across three land use types

Species	Activity level (With standard error)	Activity level comparison			
		Difference	Standard error	Wald test	p-value
Black naped hare	PA: 0.463 ± 0.012	PA vs. RF: 0.069	0.022	9.837	0.001
	RF: 0.393 ± 0.017	PA vs. FMFL: 0.100	0.018	28.446	0.000
	FMFL: 0.362 ± 0.013	RF vs. FMFL: 0.031	0.022	1.902	0.167
Golden jackal	PA: 0.463 ± 0.020	PA vs. RF: 0.069	0.037	3.340	0.067
	RF: 0.393 ± 0.031	PA vs. FMFL: 0.100	0.035	7.920	0.004
	FMFL: 0.362 ± 0.028	RF vs. FMFL: 0.031	0.042	0.530	0.466
Indian fox	PA: 0.330 ± 0.042	PA vs. RF: -0.156	0.048	10.328	0.001
	RF: 0.486 ± 0.023	PA vs. FMFL: -0.056	0.061	0.839	0.359
	FMFL: 0.387 ± 0.045	RF vs. FMFL: 0.099	0.050	3.811	0.050
Jungle cat	PA: 0.427 ± 0.060	PA vs. RF: 0.056	0.071	0.636	0.425
	RF: 0.370 ± 0.037	PA vs. FMFL: 0.008	0.061	0.017	0.895
	FMFL: 0.419 ± 0.009	RF vs. FMFL: -0.048	0.038	1.598	0.206
Sloth bear	PA: 0.413 ± 0.056	PA vs. RF: 0.003	0.065	0.003	0.952
	RF: 0.409 ± 0.032	PA vs. FMFL: 0.039	0.067	0.352	0.552
	FMFL: 0.373 ± 0.036	RF vs. FMFL: 0.036	0.049	0.537	0.463
Leopard	PA: 0.470 ± 0.085	PA vs. RF: -0.044	0.098	2.109	0.146
	RF: 0.514 ± 0.048	PA vs. FMFL: 0.084	0.866	0.090	0.028
	FMFL: 0.386 ± 0.027	RF vs. FMFL: 0.128	0.056	5.207	0.022
Wild pig	PA: 0.499 ± 0.032	PA vs. RF: -0.063	0.058	1.193	0.274
	RF: 0.563 ± 0.048	PA vs. FMFL: 0.052	0.038	1.886	0.169
	FMFL: 0.446 ± 0.020	RF vs. FMFL: 0.116	0.052	4.908	0.026

Abbreviations: Protected Area 'PA', Reserved Forest 'RF', fringe mosaic farmland 'FMFL', Wald test to check if estimates are significantly different from 0

Thus, our results that two existing sloth bear sanctuaries in the district were placed in locations that are highly valuable for bear conservation. Relative abundance of humans was positively associated with the habitat use of jungle cats which could be due to their strong dependence on the availability of small prey like rodents that are mostly found in human-modified landscapes (Mukherjee et al. 2004). The habitat use of foxes was negatively associated with proximity to scrub forest and landscape rockiness. Higher habitat use of foxes and jackals in RFs relative to PAs maybe be explained by two factors. First, the moderately disturbed landscape of RFs might provide additional food resources (Jaegar et al. 2007) as well as reducing the frequency of encounters with large predators. Second, the RFs in our study area are associated with the plain landscapes and that feature could provide suitable sites for denning (Carricondo-Sanchez et al. 2019; Kumara and Singh 2012). Wild pigs are heavily poached throughout our study site (Behera et al. 2022) which likely explains their negative response to increased RAI human. The habitat use of two large mammals in our study i.e. leopard, and sloth bear, were positively influenced by the canopy coverage, which concurs with the findings of prior studies (Ngoprasert et al. 2007; Whitworth et al. 2019). According to Gould et al. (2001), high termite densities are associated with cattle dung patches, which explains our identification of RAI cattle as a strong positive predicting factor for sloth bear habitat use.

We found the mean annual precipitation was one of the important predictor variables for habitat use by five mammals. Precipitation positively influenced the habitat use of leopards, wild pigs, and hares but it was negatively associated with the habitat use of jackals and foxes. This affirms strong relationship of precipitation with the distribution of these mammals in dry landscapes (Ogutu and Owen-Smith 2005; Yusefi et al. 2021). With increased human activities, more species inhabit modified landscapes consisting of a mosaic of both natural and anthropic land covers. The ability of species to adapt and use anthropic land covers is a key determinant of their persistence in human-modified landscapes (Galán-Acedo et al. 2019).

Intensification of human disturbances causes wild mammals to avoid direct confrontation with humans to survive (Ditchkoff et al. 2006). Human disturbances and presence have negative effects on many mammals causing them to avoid disturbed landscapes, suppress their activity levels, or alter their activity patterns (Ikeda et al. 2022; Oriol-Cotterill et al. 2015; Suraci et al. 2021). With human activities being primarily diurnal in our study area, all species showed nocturnal activity patterns. We found that species with larger body sizes like leopards, bears, and wild pigs increased nocturnal activity pattern in more disturbed land-use type like FMFL relative to PAs/RFs, which is consistent with earlier studies (Carter et al. 2015; Johann et al. 2020; Ohashi et al. 2013; Ramesh et al. 2013; Van Cleave et al. 2018;). Meso-predators like jackals and foxes increased diurnal activity in RF or FMFL relative to PA. Sunquist and Sunquist (2002) found that jungle cats are typically diurnal. However, in our study jungle cat exhibited nocturnal activity patterns in all land use types. This difference in our data maybe a response to the high intensity of human disturbance across our study area. Activity patterns of jackals, foxes, and jungle cats across land-use types may relate to their tolerance of human presence. Hare had similar activity patterns across land-use types, but we observed a spike in their activity patterns in RFs and FMFL. Hares' activity pattern varies from crepuscular to nocturnal, and their increased activity in the twilight period suggests an increased concentration of activity in human modified landscapes. We also observed a shorter window in their activity patterns within human-dominated landscapes (Shamoon et al. 2018). Estimates of activity level of four out of seven of our study species showed higher activity in PAs or RFs than in FMFL suggesting wild mammalian species prefer spending more time in less-disturbed landscape. Thus, our mammalian activity-related results supported our prediction that mammalian species would show increased nocturnal activity patterns in FMFL relative to PAs/RFs and increased concentration of activity i.e., a shorter activity of window with increasing habitat disturbance.

Our study provided novel insights into the complex relationship between anthropogenic disturbance and mammalian assemblage by quantifying the filtering effect of human land use change on seven mammal species with diverse traits (Belote et al. 2020; Hill et al. 2020). Our consideration of several land use variables provides quantitative insights to inform strategic decision-making in the conservation of mammals. Even though our analyses focused on the

Deccan plateau of India, we strongly advocate that the patterns observed are likely applicable to medium-to-large mammal species globally. For example, a shift in mammal community composition towards smaller and generalist species with reduced space requirements can be a consequence of the increasing the human footprint (Suraci et al. 2021). The structure and diversity of mammal communities are the key determinants of ecosystem processes (Estes et al. 2011; Schmitz et al. 2018). However, more studies need to investigate the links between functional traits and habitat use of species in different land use types. Similar studies which also incorporate inter-specific interaction along environmental gradients will provide more robust information about ecosystem function. Conservationists and wildlife managers are typically focused on the protection of wildlife species in PAs. Given that the majority of species reside outside PAs, our results highlight the shortcomings of the forest PA network. Despite being detrimental to many species, semi-disturbed non-protected areas like RFs, provide opportunities for some species to prosper while also connecting PAs (Berger 2007). Expanding PAs will certainly help the populations of large mammals (Milda et al. 2023), but for species that thrive outside PAs, we recommend new studies determining their habitat requirements to provide effective refuge areas for conservation (Li et al. 2021). Conservation objectives require approaches for managing landscapes holistically by incorporating anthropogenic habitats like RFs, and farmlands with PA networks.

Ongoing landscape modification and increasing human use of remaining natural areas make it important to identify species that will thrive as well as those that will perish under anthropogenic pressure. Such inference is critical to conserving mammal communities and to maintaining mammalian diversity and associated ecological services. Natural habitats in a mosaic of anthropic-modified habitats can reduce negative effects on wildlife (Ehlers Smith et al. 2018; Galán-Acedo et al. 2019). Therefore, forest patch protection should be encouraged through continued reforestation and restoration, which will benefit a diverse range of mammalian species. Regulation of mining activities and mining-vehicular movements inside forests along with a strict enforcement of rules related to illegal resource extraction such as overgrazing and poaching activities could further reduce adverse effects on wildlife. So, we advocate for new studies that analyze the effects of mining related activities, overgrazing, and poaching on wildlife conservation in Ballari district We urge conservation agencies to increase awareness by organizing training programs for local communities. Such programs should improve understanding of human-wildlife interactions while providing suitable incentives and compensation to people who suffer wildlife damage. Our findings illustrate the need for conservationists, forest managers, and local people to work together to create landscape-level planning that integrates local livelihoods and wildlife conservation.

Declarations

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