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Jungle Cats and Leopard Cats: Distribution, Occupancy Modeling, and Activity Patterns in Bardia National Park, Nepal

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ABSTRACT

Small cats play a vital role in maintaining ecological balances. Inadequate knowledge based on their habitat preference and interspecific competition has hindered the effective conservation initiatives. We studied occupancy and diel activity patterns of two sympatric small cats, i.e., jungle cat (*Felis chaus*) and leopard cat (*Prionailurus bengalensis*), in and around Bardia National Park (BNP) using camera trap data. BNP was divided into 344 camera trap grids of 2×2 km, and a survey was conducted with a trapping effort of 6307 days. For the occupancy modeling, we applied a single-species single-season occupancy model. We analyzed 11 covariates that have the potential to influence the occupancy of jungle cats and leopard cats. The probability of occupancy of the jungle cat was 0.17 (SE: 0.0026, CI: 0.1726, 0.18271). The tiger's index positively influenced the jungle cat's occupancy, while it showed a strong negative association with the terrain ruggedness index and distance to road. Similarly, the probability of occupancy for leopard cat was found to be 0.19 (SE: 0.0022, CI: 0.1829, 0.1916). The leopard cat occupancy was strongly positively correlated with riverine forest habitat type. We used non-parametric kernel-density functions on camera trap data to determine diel activity patterns. Sympatric jungle cat and leopard cat showed high temporal overlap with a coefficient ($\Delta = 0.9$), being nocturnal. The distribution of jungle cats and leopard cats in BNP appears to be facilitated by spatial segregation. The study serves as a baseline for further research and conservation initiatives for these two sympatric cats in western Nepal.

1 | Introduction

Understanding how sympatric carnivores use space, habitat, and time is essential for interpreting their ecological roles and for developing effective conservation strategies in multi-predator systems (Farris et al. 2016). Patterns of spatial and temporal habitat use among co-occurring species may arise from shared resource requirements, differential habitat preferences, or responses to environmental pressures such as human disturbance or large carnivores (Araújo and Luoto 2007; Willems and Hill 2009; Farris et al. 2016). Species with similar ecological requirements potentially overlap in the use of food resources (Putman and Putman 1996; Donadio and Buskirk 2006). Apex predators include keystone species that play fundamental roles in ecosystems through direct and/or indirect effects on organisms belonging to lower trophic levels (Ripple et al. 2014). Theoretically, if the availability of shared resources is not a limiting factor, species would coexist without competing. Conversely, if the availability of resources is limited, competition is expected to occur: one species, the 'superior' competitor, affects the 'inferior' competitor through resource exploitation or interference (De Boer and Prins 1990;

Putman and Putman 1996). And these associations can influence population dynamics, habitat use, and activity patterns of small carnivores with potential effects on trophic levels (Crooks and Soule 1999; Palomares and Caro 1999; Ripple et al. 2014). Therefore, the two forces, the environmental factors and the presence or absence of other species, heavily influence where a species occurs (Fox-Rosales and de Oliveira 2023). Among carnivores, these dynamics are particularly critical because they naturally occur at low densities due to their apex or mesopredator positions within food webs (Karanth and Chellam 2009).

Asia holds more than 60% of the global diversity of cats (Macdonald et al. 2010), harboring 21 out of 36 species (Chatterjee et al. 2020). Nepal, a mega-biodiverse country (Paudel et al. 2012), is home to 13 species of felids, including 4 big cat species and 9 small cat species, making it the second richest country in the world for felid diversity after India (Dickman et al. 2015; Lamichhane et al. 2023).

Jungle cats (*Felis chaus*, Figure 1) and leopard cats (*Prionailurus bengalensis*, Figure 1) both exhibit non-uniform spatial distributions that reflect their reliance on specific habitat types. Jungle cats typically occur in deciduous forests, riparian vegetation, and areas with permanent water sources (Gray 2021), while also demonstrating adaptability to various agricultural landscapes where rodent prey is abundant (Ogurlu et al. 2010). In contrast, leopard cats more frequently prefer natural forests and shrublands, but also tolerate agricultural areas with moderate human disturbance (Mohamed et al. 2013; Shanida et al. 2023). Both species are currently listed as Least Concern on the IUCN Red List and are sympatric across wide portions of their geographic ranges (Gray 2021; Ghimirey et al. 2023). These species have been found below 4500-m elevation in Nepal (Jnawali et al. 2011). They regulate prey populations and facilitate nutrient transfer, serving as crucial components of terrestrial food webs (Bandyopadhyay et al. 2024). Despite their ecological significance, only a few records are available about their distribution and preferred habitats in Nepal (Aryal et al. 2018; Lamichhane et al. 2023).

Within the Bardia National Park (BNP), mostly the studies have been focused on big cat species (Odden and Wegge 2005; Tamang and Baral 2008; Bhattarai 2009; Grey 2009; Deo 2014; Upadhyaya et al. 2018; Shah et al. 2024). Few studies, including opportunistic records of small cat species, have been carried out so far in BNP (Yadav et al. 2018), leaving a major research gap on small cats. In BNP, where the tiger (*Panthera tigris tigris*) population is 125 and density is the highest in Nepal (DNPWC and DFSC 2022), the presence of these large carnivores may significantly affect the occurrence of jungle cats and leopard cats (Sunarto et al. 2015). Apex predator like tigers can affect mesocarnivores through lethal association involving intraguild predation or non-consumptive killing (Palomares and Caro 1999; Donadio and Buskirk 2006). Importantly, sympatric jungle cats and leopard cats are often preyed upon by larger carnivores, including leopards (*Panthera pardus*) (Baral et al. 2022), and dholes (*Cuon alpinus*) (Kamler et al. 2020) Furthermore, the fear of tigers can also influence the behavior and ecology of small cats, which are expected to avoid larger ones, leading to spatial/temporal partitioning (Palomares et al. 1996; Durant 1998; Karanth et al. 2017). Some studies found high spatial overlap between both small cat species and large felids (Sunarto et al. 2015; Kyaw et al. 2021), whereas another study (Vitekere et al. 2020) revealed that small cats avoided large felids. In Nepal, large cats are known to coexist with other small-to medium-sized predators through niche differentiation, by killing the prey of different sizes as a form of niche segregation (Sharma et al. 2024). While the co-existence of humans with these cat species can reduce human-rodent conflicts as they feed on rodents in human-occupied areas (Mahato et al. 2023). However, loss and fragmentation of natural habitats from human activities can restrict their movements, disrupt foraging patterns, and limit access to prey. Human activities also result in potential threats to jungle cats and leopard cats, including poaching and trapping (Duckworth et al. 2005) and collision with vehicles (Solanki et al. 2017; Kim et al. 2019; Kumawat and Purohit 2020), which can directly impact populations. Therefore, it is urgently required to assess the factors influencing the habitat use of these small cats. Traditional presence-absence (or detection-only) data may underestimate true occupancy and provide limited guidance for conservation planning because they fail to account for imperfect detection (MacKenzie 2005b; Kéry 2011). Therefore, occupancy modeling offers a robust framework to address this gap by utilizing detection-non-detection data (MacKenzie 2005a; Kéry 2011; Williamson et al. 2021).

FIGURE 1 | Camera trap captured photographs from the study area; on the left is the jungle cat, and on the right is the leopard cat.

This study aims to (1) map the distribution of jungle cats and leopard cats across BNP and its associated forest using camera trap data and spatial modeling, (2) assess how environmental factors, anthropogenic disturbances, and the activity of a top predator (tiger) influence the occupancy, and (3) examine diel activity and temporal overlap of two sympatric jungle cats and leopard cats. By integrating spatial and temporal dimensions of habitat use, this research contributes to a more nuanced understanding of small felid ecology in a tiger-dominated conservation landscape and provides actionable insights for inclusive carnivore management in Nepal.

2 | Materials and Methodology

2.1 | Study Area

Bardia National Park (BNP) is the largest national park in the southern plain area (Terai) bordering India (N: 28.2630 to 28.6711; E: 80.1360 to 81.7645), which covers an area of 968 km^2 with its buffer zone comprising an area of 507 km^2 (Figure 2). BNP and its buffer zone connect to the Banke National Park (BaNP) in the east and to Katarniaghat Wildlife Sanctuary in India in the south through the Khata forest corridor. BNP is a part of the Terai Arc Landscape (TAL), a transboundary tiger conservation landscape in India and Nepal, identified as a Level 1 tiger conservation unit (Wikramanayake et al. 1998). BNP has monsoon (June–September), winter (October–February), and summer (March–May) seasons. The mean monthly temperature ranges from a minimum of 10°C to a maximum of 45°C. The park receives a mean annual rainfall of ~1700 mm (Thapa et al. 2022).

BNP consists of subtropical vegetation with riverine forest, riverine floodplain grassland along the two major rivers (Karnali and Babai rivers), sal (*Shorea robusta*) forest with interspersed grassland, and mixed hardwood forests (Dinerstein 1979). The park holds the highest density of tigers in Nepal, with an estimated density of ~7 individuals 100 km^2 and an estimated prey density of ~90 individuals km^2 (DNPWC and DFSC 2022). The major predators of BNP are tiger, common leopard, striped hyena (*Hyaena hyaena*). Prey species such as spotted deer (*Axis axis*), hog deer (*Axis porcinus*), wild boar (*Sus scrofa*), barking deer (*Muntiacus vaginalis*), and swamp deer (*Rucervus duvaucelii*) are found in this area (Wegge et al. 2009). Other species such as dhole, golden jackal (*Canis aureus*), fishing cat (*Prionailurus viverrinus*), and sloth bear (*Melursus ursinus*) (Yadav et al. 2017, 2019) are associated carnivores in the park. Mega herbivores like the greater one-horned rhinoceros (*Rhinoceros unicornis*) and the Asian elephant (*Elephas maximus*) are also present in the area.

2.2 | Data Collection

We used camera-trapping data collected by the Department of National Parks and Wildlife Conservation (DNPWC), Nepal, during the national tiger surveys conducted in 2022 in BNP. During the survey, systematic camera trap methods were applied in BNP and its associated buffer zone area for monitoring of tigers (DNPWC and DFSC 2022). The monitoring was carried out from 16 December 2021 to 27 January 2022 following the tiger monitoring protocol of Nepal (DNPWC 2017; DNPWC and DFSC 2022). The study area was divided into grids of size 2 km x 2 km, and a total of 344 grid cells were

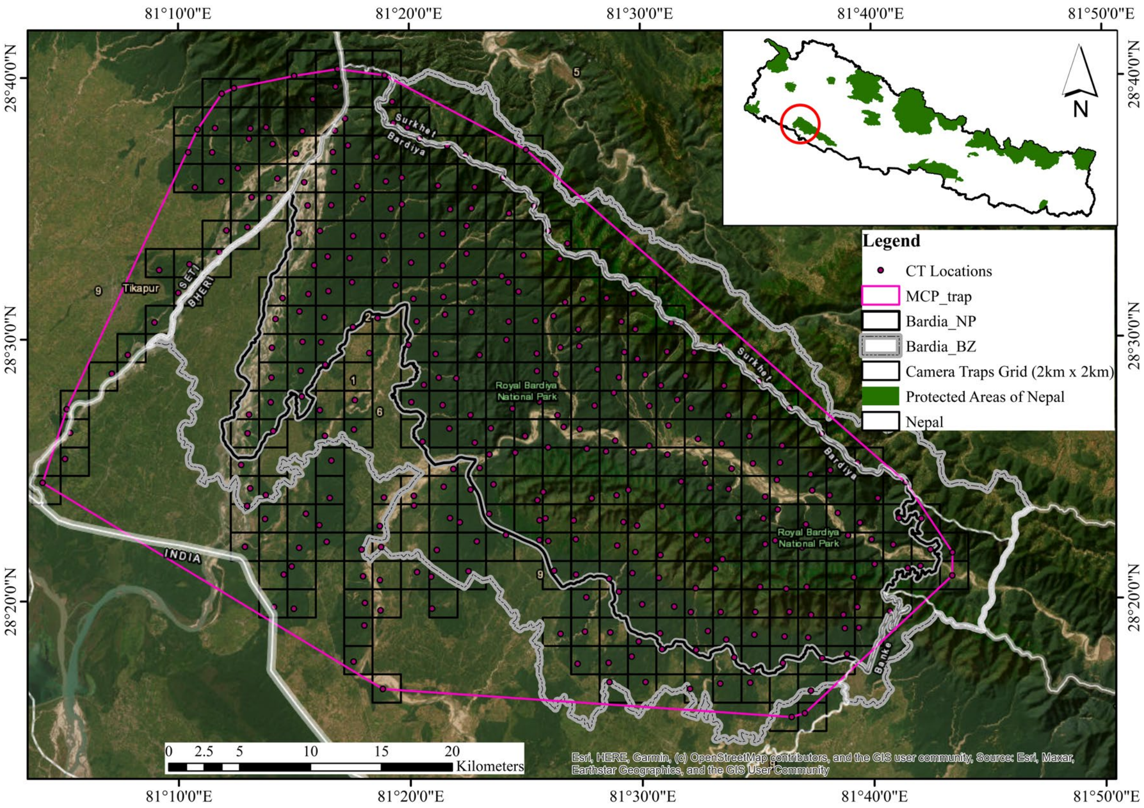

FIGURE 2 | Map of Bardia National Park and its associated forests area with camera trapping grids and camera trap locations.

surveyed. Due to the limited number of cameras available for the survey, the trapping was carried out in shifting blocks (DNPWC and DFSC 2022). Here in BNP and its associated forest area, two blocks (block 1 = 191 grids and block 2 = 153 grids) were formed. In each grid, a pair of cameras was placed for at least 15 nights (ranging from 15 to 20 nights). The camera traps were deployed in strategic locations such as fire lines, trails, riverbanks, ridge lines, and forest roads to maximize the detectability of tigers (Karanth et al. 2011). To capture both flank and full body coverage of tigers, two camera traps were mounted on wooden posts or tree trunks at a height of 45–60 cm above ground level and spaced 4–8 m apart on either side of those strategic locations (Karanth and Nichols 2002; DNPWC and DFSC 2022). Automated cameras such as Cuddeback (C1) and Panthera (V5 and V6) were used to obtain high-quality images. The cameras were programmed to take three pictures per trigger with no delay (FAP mode). Regular maintenance, such as camera checks, was performed on each camera trap to ensure functionality, and images and metadata were retrieved on a weekly basis and stored safely. From the survey data, we extracted the photographs of jungle and leopard cat and prepared the detection history of the surveyed grid. We used the 2 × 2 km grid framework because previous studies (Selvan et al. 2014; Srivathsa et al. 2015; Aryal et al. 2018; Chatterjee et al. 2020; Sharma et al. 2024) have successfully used similar grid sizes to assess the occupancy of the small cats, ensuring methodological consistency and comparability with existing research.

2.3 | Data Analysis

2.3.1 | Occupancy Modeling

2.3.1.1 | Covariate Selection. For the analysis, the combination of 11 remote sensing and ground-based variables (Table 1) was taken in a way that habitat conditions, anthropogenic pressures (if any), and the overall characteristics of the landscape were reflected.

The details about the camera trap model and habitat types were extracted from the camera trap deployment datasheet. The habitat types: mixed forest (MF), sal forest (SF), riverine forest (RF), and tall grassland (TG) were classified based on visual assessments conducted by the survey team during camera trap deployment. The survey grid was assigned a specific habitat type if that habitat covered more than 50% of the grid's land area (Shah et al. 2025). The location of waterholes (man-made water sources constructed by the park authority as a part of habitat management) was retrieved from the National Trust for Nature Conservation (NTNC), and the distance to the camera trap was calculated using the near tool in ArcGIS. Similarly, the shapefile of river channels, settlement and roads were downloaded from National Spatial Data Center: Geoportal (https://nationalgeoportal.gov.np/#/), and distance to camera trap was calculated using the Spatial Analyst Tool extension of ArcGIS v.10.5. The Above Ground Biomass (AGB) was downloaded from Global Forest Watch (https://data.globalforestwatch.org/datasets/gfw::aboveground-live-woody-biomass-density/about) at the scale of approximately 30 m and used for the analysis (Global Forest Watch 2022). The downloaded AGB was overlaid with the 2 km x 2 km grid, and the mean AGB value within each grid cell was calculated and used as site-level covariates. Likewise, Topographic heterogeneity was measured using the Terrain Ruggedness Index (TRI) developed by (Riley et al. 1999) using the Digital Elevation Model (DEM) data within 30 s (approx. 1 km resolution) downloaded from WorldClim (https://www.worldclim.org/data/worldclim21.html). The average value of TRI for each grid was calculated and used for the analysis (Mukherjee et al. 2013; Thapa et al. 2019). We derived the tiger index, leopard cat index, and jungle cat index from the camera trap survey data. The tiger index reflects the capture rate of the tiger, calculated as the number of photo events per 100 trap nights. The photos of the tiger taken within 30 min at a camera location were considered a single photo event (Carter et al. 2012; Shah et al. 2024). To assess the influence of sympatric cats on each other, we also calculated the leopard cat index and jungle cat index, following the method that was used to obtain the tiger index.

We standardized all continuous covariates using the z-transformation methods to ensure consistency, comparability, and checked multicollinearity using the corrplot package in R (Wei and Simko 2010) among predictors before running occupancy models (Sunarto et al. 2012; Kafley et al. 2016; Shah et al. 2025). Between two highly correlated variables, ecologically less meaningful covariates were excluded in the model-building procedure (Pearson's $|r| = > 0.7$) (Lamichhane et al. 2021; Sharma et al. 2024). In our correlation test, no variables were highly correlated, so we didn't remove any variables during the model formation.

2.3.1.2 | Statistical Analysis. For the occupancy modeling of both the jungle and leopard cats, we used a single-species single-season occupancy model, as it uses detection-non-detection data for robust estimates of the probability of use and accounts for imperfect detections, e.g., (MacKenzie et al. 2002, 2006). All statistical analyses were performed using the “unmarked” package (Fiske and Chandler 2011; Kellner et al. 2023) in R Version: 2025.05.1 + 513.

For the detection history of both cat species, the detection and non-detection of both species were recorded, implying 1 as detection and 0 as non-detection. The days when cameras were inactive were coded as NA, not as non-detection. One day (24 h) was taken as one sampling occasion. Within a grid if only one camera in a pair was operating, the station was still treated as active and detection was recorded based solely on the functioning camera. First, the covariates were modeled for detection probability “p”, where we assumed the parameters to be constant or allowed to vary as covariates, while site use probability (ψ) was held constant in a general model (MacKenzie et al. 2006).

Covariates were assigned to the ψ, or p components, based on their expected biological mechanism. Variables representing broad-scale ecological conditions (e.g., habitat type, distance to waterholes, roads, settlements, terrain ruggedness, tiger index, and jungle cat index/leopard cat index) were considered potential occupancy covariates. However, because these same features can also affect animal movement patterns, visibility, and sensor performance at the camera location, they were also evaluated as potential detection

TABLE 1 | List of covariates used for occupancy modeling of jungle cat and leopard cat.

Types	Covariates	Rationale
Categorical	Habitat	Jungle cats are known to prefer tall grass, thick brush, riverine swamps, and reed beds, while leopard cats are found to prefer mixed deciduous and dry evergreen forest habitats in association with water courses in South Asia (Sunquist and Sunquist 2002). So accordingly, we recorded the habitat types throughout our study area during the deployment of the camera traps
	Camera models	The sensor sensitivity, trigger speed, angle of coverage, detection range, and image processing capabilities of the camera vary with its models. These differences in the camera's features affect the ability of the camera models to detect and capture the photographs of the species (Thapa et al. 2024). So, we took camera models as one categorical covariate
Continuous	Distance to River	Water becomes the critical limiting factor in BNP during the dry season (Shah et al. 2025). Also, bed reeds of riverbanks and dry streams serve as important prey resources for both species (Rostro-García et al. 2021). So, the preference of the jungle cat and leopard cat towards riverine areas in BNP needs to be assessed
	Distance to Road	Roads are linked with direct animal mortality and landscape fragmentation, causing barriers to animal movement (Coffin 2007)
	Distance to Waterholes	In dry months, the natural sources of water in BNP dry up, and waterholes play an important source of water (Shah et al. 2025)
	Distance to Nearest Settlement	Distance to human settlements serves as a crucial factor for anthropogenic influence and disturbance. While closer proximity might offer ecological opportunities such as food subsidies or accessible prey, this benefit is offset by an increased risk of escalating human-wildlife conflict, direct persecution, and habitat degradation (Penjor et al. 2022)
	Above Ground Biomass	AGB signifies the availability of dense cover, which is vital for these ambush predators like jungle cat and leopard cat for stalking prey and for refuge from larger predators and human disturbance (Sunquist and Sunquist 2002). This dense vegetation also creates diverse microhabitats supporting a higher prey abundance, like rodents, birds (Dorigo et al. 2021)
	Topographic Ruggedness Index	Leopard cats are found to prefer steep slopes as per (Lim et al. 2015), while jungle cats are found to prefer plains and lowlands, particularly areas with grasslands, wetlands, and dense cover (Sunquist and Sunquist 2002)
	Tiger Index	The presence of apex predators like tigers can impact jungle cats and leopard cats in areas where their habitats overlap. Therefore, tiger occurrence was included as a site-level covariate to evaluate whether the presence of a tiger influences the habitat use of jungle cats and leopard cats. As a result, larger carnivores may influence the smaller cats' behavior, habitat preferences, and distribution patterns (Lynam et al. 2013)
	Leopard cat index (for jungle cat)	As both the jungle cat and the leopard cat are of similar size and prefer similar prey species, they share a similar feeding niche (Rostro-García et al. 2021). The way sympatric jungle cats and leopard cats exist together in the same areas, both spatially and temporally, is shaped by their habitat preferences and how they compete. Understanding these factors is crucial for developing effective conservation strategies (Sharma et al. 2024)
	Jungle cat index (for leopard cat)	As both jungle cat and leopard cat are of similar size and prefer similar prey species, they share a similar feeding niche (Rostro-García et al. 2021). The way sympatric jungle cats and leopard cats exist together in the same areas, both spatially and temporally, is shaped by their habitat preferences and how they compete. Understanding these factors is crucial for developing effective conservation strategies (Sharma et al. 2024)

covariates. This dual consideration follows standard occupancy-modeling guidelines when the influence of specific covariates on ψ versus p is uncertain. ψ was modeled by first selecting the best detection model identified previously and then testing all possible combinations of site use covariates. Model selection was based on the Akaike Information Criterion (AIC) adjusted for small sample sizes (MacKenzie et al. 2006). The model with the lowest $\Delta\text{AICc} = 0$ was considered the best-fitting model. Models within $\Delta\text{AICc} < 2$ were considered to have substantial support and were regarded as equally plausible, whereas models with $\Delta\text{AICc} > 10$ were considered unsupported. Final estimates of site use probability and detectability were obtained by model averaging across competing models (Burnham and Anderson 2002). Additionally, β estimates of covariates were computed to assess the magnitude and direction (positive or negative) of their influence on-site use and detection probability. Also, we assessed goodness-of-fit (GOF) for the top occupancy model of each species using a parametric bootstrap GOF test (MacKenzie and Bailey 2004). Model fit and overdispersion were quantified using the $\hat{c}$ statistics ($\hat{c} = X^2$ observed/X^2 simulated) at 1000 bootstrap simulations. Values of $\hat{c} = 1$ indicate adequate fit, whereas values substantially > 1 indicate overdispersion (Payne et al. 2018). The estimated overdispersion parameters were $\hat{c} = 0.434$ for leopard cats and $\hat{c} = 0.433$ for jungle cats, indicating no dispersion and confirming that the model structure was appropriate.

2.3.2 | Diel Activity Patterns Analysis

We used non-parametric kernel-density functions (Ridout and Linkie 2009) to determine the daily activity periods of both cats from the camera-trap photo captures (Li et al. 2022). Independent capture events were used to calculate the density function. We considered two capture events independent if the time between consecutive photographs of one species from the same camera traps had a time interval of 30 min (Rabinowitz 1990; Kelly and Holub 2008; Chatterjee et al. 2020). We used the "overlap" package (Meredith and Ridout 2014) in R to understand the temporal activity overlap between the cats. This method generates a coefficient of overlap between 0 and 1, indicating the complete temporal separation between two species at 0 and complete overlap at 1 (Ridout and Linkie 2009). We considered $\Delta > 0.8$ to be a strong overlap and $0.5 < \Delta < 0.8$ as a moderate overlap (Lynam et al. 2013). We used the Δ_4 estimator (Dhat4) for sample sizes > 75 and the Δ_1 estimator (Dhat1) for smaller sample sizes, < less than 50, following the recommendations provided by (Meredith and Ridout 2014). Both species had > 75 independent detections (151 for jungle cat and 126 for leopard cat); therefore, we used Δ_4. Confidence intervals for the activity density curves were generated via 1000 bootstraps, but no bootstrapping was applied to Δ, for which we report the point estimate.

3 | Results

A total of 6307 trap nights were conducted at 344 stations, resulting in leopard cat detection at 46 stations and jungle cat detection at 49 camera trapping grids (Figure 3). For leopard cats, 34 were recorded in mixed forest, 7 were in riverine forest, and the remaining were in sal forest. Similarly, jungle cats were detected at 21 camera stations within mixed forest, 19 in sal forests, 8 in riverine forests, and 1 in tall grassland habitat.

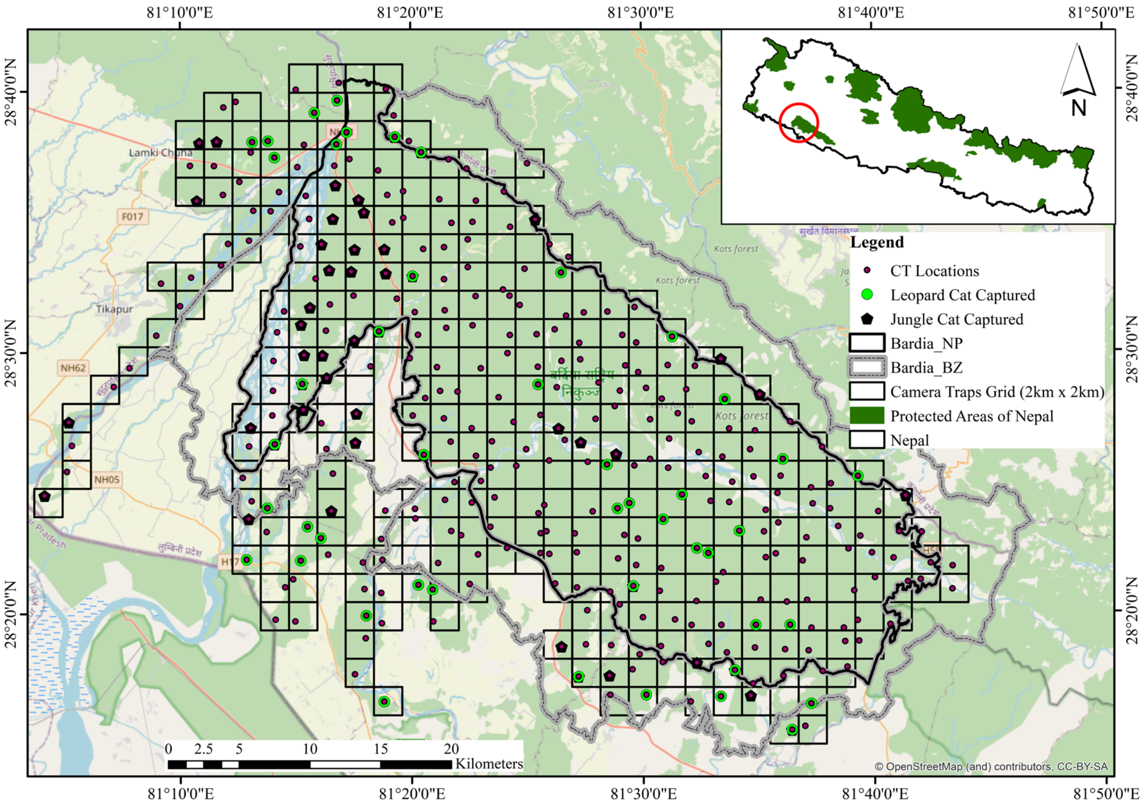

FIGURE 3 | Spatial distribution map of jungle cat and leopard cat in BNP and its associated forest area.

3.1 | Modeling Probability of Detection

3.1.1 | Jungle Cat

The detection probability of the jungle cat in BNP and the associated forest area was 0.081 (SE: 0.0009, CI: 0.0797, 0.08360). Habitat type was the most influential covariate for the detection probability of the jungle cat (Table 2). The jungle cat had a high detection probability in the riverine forest followed by the sal forest habitat type (Figure 4).

Riverine forest ($\beta = 0.865$ SE ± 0.357) and sal forest ($\beta = 0.768$ SE ± 0.3) had a higher detectability of jungle cats compared to mixed forest ($\beta = -2.76$ SE ± 0.253) and tall grassland ($\beta = -0.831$ SE ± 0.001) (Figure 4). Also, the detection probability of jungle cats was negatively associated with the distance to waterholes ($\beta = -0.204$ SE ± 0.001). In contrast, distance to settlements ($\beta = 0.0293$ SE ± 0.009) was positively associated with the detection of jungle cats. We found Panthera ($\beta = 0.271$ SE ± 0.0002) camera traps performed better compared to Cuddeback ($\beta = -2.4$ SE ± 0.226) and Reconyx ($\beta = -7.252$ SE ± 2.664) cameras for detecting jungle cats (File S1).

TABLE 2 | Summary of the model selection procedures for factors influencing the effect of the fine-scale covariates on jungle cat detection probability.

Models	K	AIC	ΔAIC	AICwt	cumltvWt
p (Habitat) ψ (.)	5	918.67	0	0.689	0.69
p (waterholes) ψ (.)	3	921.56	2.89	0.162	0.85
p (.) ψ (.)	2	922.8	4.13	0.087	0.94
p (settlement) ψ (.)	3	924.75	6.08	0.033	0.97
p (Camera Model) ψ (.)	4	925.1	6.43	0.028	1

Note: AIC = Akaike information criterion, AIC wt. = the AIC model weight, K = Number of model parameters including intercepts and covariates, ΔAIC = the difference in AIC values between each model and the model with the lowest AIC, ψ = the probability of occupancy, Habitat = Types of Habitats, waterholes = Distance to waterholes, settlement = Distance to settlement, Camera Model = Types of camera model used in the survey.

3.1.2 | Leopard Cat

The detection probability of leopard cats in BNP and the associated forest area was 0.07 (SE: 0.0013, CI: 0.0703, 0.0754). Distance to the waterholes was found to be the most influential covariate for the detection probability of leopard cat, and the second most influential was the distance to the river (Table 3).

We found that the detection probability of leopard cats was negatively associated with the distance to waterholes ($\beta = -0.203$ SE ± 0.1691). Sal forest ($\beta = 0.052$ SE ± 0.004) was a better habitat compared to the riverine forest ($\beta = -0.44$ SE ± 0.047), mixed forest ($\beta = -1.7233$ SE ± 0.219) and tall grassland ($\beta = -7.411$ SE ± 0.612) for detecting leopard cats (Figure 5). We found that Panthera ($\beta = 0.007$ SE ± 0.337) camera traps performed better compared to Cuddeback ($\beta = -1.796$ SE ± 0.237) and Reconyx ($\beta = -5.301$ SE ± 21.118) camera traps for detecting leopard cats (File S2).

3.2 | Probability of Occupancy

We used detectability models in subsequent analyses to model occupancy probability (Tables 4 and 5). We fitted 29 (13 jungle cat and 14 leopard cat) occupancy models with combinations of covariates to estimate the occupancy of these two species.

3.2.1 | Jungle Cat

The naïve occupancy of jungle cat was found to be 0.14 and the occupancy probability was 0.17 or 17% (SE: 0.0026, CI: 0.1726, 0.18271). Among the evaluated models, the model with the habitat types and terrain ruggedness index, tiger, and road "p (Habitat) ψ (TRI + Tiger + road)" had the highest rank (ΔAIC = 0) (Figure 6). The covariates TRI, tiger, road, and habitat together were valuable

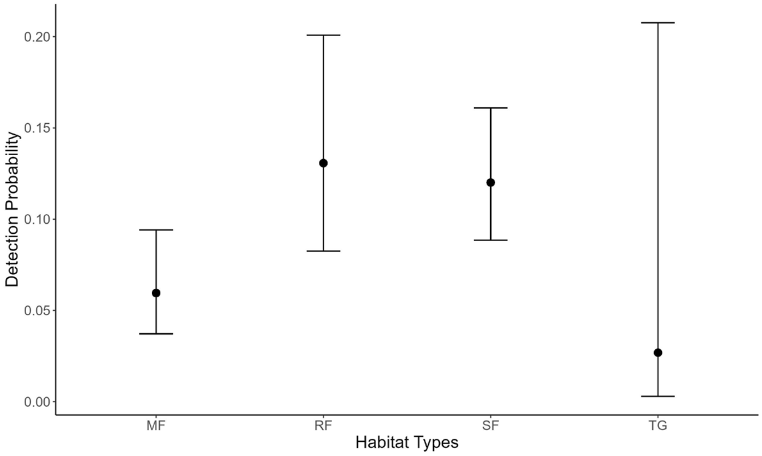

FIGURE 4 | Relationship between the habitat types in the grids and the detection probability of the jungle cat. MF, Mixed Forest, RF, Riverine Forest, SF, Sal Forest, TG, Tall Grass.

TABLE 3 | Summary of the model selection procedures for factors influencing the effect of the fine-scale covariates on leopard cat detection probability.

Models	K	AIC	ΔAIC	AICwt	cumltvWt
p (waterholes) ψ (.)	3	577.91	0	0.45	0.45
p (river) ψ (.)	3	579.01	1.1	0.26	0.72
p (Habitat) ψ (.)	5	579.76	1.86	0.18	0.89
p (CameraModel) ψ (.)	4	580.83	2.92	0.11	1

Note: AIC = Akaike information criterion, AICwt. = the AIC model weight, K = Number of model parameters including intercepts and covariates, ΔAIC = the difference in AIC values between each model and the model with the lowest AIC, ψ = the probability of occupancy, Habitat = Types of Habitats, waterholes = Distance to waterholes, Camera Model = Types of camera model used in the survey, river = Distance to river.

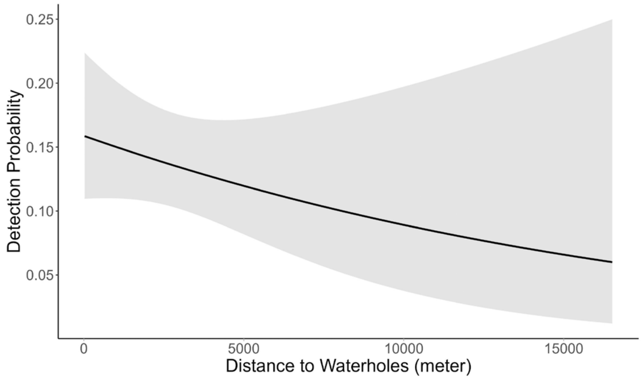

FIGURE 5 | Relationship between the distance to the waterholes from the grids and the detection probability of the leopard cat.

for estimating jungle cat occupancy (Table 4). Jungle cats were found to be dominant in the southwestern, north central, and southeastern zones of BNP and its buffer zone (File S3).

3.2.2 | Leopard Cat

The naïve occupancy of the leopard cat was found to be 0.13, and its occupancy probability in BNP was 0.19 or 19% (SE: 0.0022, CI: 0.1829, 0.1916). The covariate waterholes and habitat "p (waterholes) ψ (Habitat)" had the highest rank (ΔAIC = 0), making it the most influential parameter for the occupancy of the leopard cat (Table 5 and Figure 7). Riverine forest ($\beta = 0.063$ SE ± 0.528) was the preferred habitat for the leopard cat, followed by mixed forest type ($\beta = -1.032$ SE ± 0.267) (Figure 7, File S2). Leopard cats were dominant in the southern, southwestern, and southeastern areas of Bardia, while they occurred moderately across central and eastern regions, with lower probabilities in the north (File S4).

3.3 | Diel Activity Patterns of Jungle Cat and Leopard Cat

Both the sympatric jungle and leopard cat showed primarily nocturnal to crepuscular behavior (Figure 8). The activity began increasing around 11:00, peaked around 20:00, and remained high into the night before declining after midnight, suggesting both species are most active from late afternoon (~16:00) to late night (~01:00), with peak activity during the early night hours. The temporal overlap coefficient ($\Delta = 0.9$) indicates a high overlap, with both species active at similar times, especially during dusk and early night. Overall, 39.41% of jungle cat activity and 36.82% of leopard cat activity occurred during the daytime, indicating that both species are predominantly nocturnal, with jungle cats being slightly more active during the day.

4 | Discussion

Our study provides one of the first detailed insights into the spatial distribution, occupancy, and activity patterns of jungle cats and leopard cats in BNP and its associated forest area. We found relatively low naïve occupancy for both species (0.14 for jungle cats and 0.13 for leopard cats). Also, the model-averaged occupancy estimate for jungle cats was 0.17 (SE: 0.0026, CI: 0.1726, 0.18271) and leopard cats was 0.19 (SE: 0.0022, CI: 0.1829, 0.1916). Despite their widespread distribution in the area, our results suggest that these two sympatric small cats occur at relatively low occurrence probabilities in BNP, with distinct habitat preferences and resource associations shaping their presence. Low estimated occupancy may partly reflect methodological constraints, including camera placement primarily optimized for tigers, species-specific differences in detectability, which can reduce camera performance for small-bodied felids. Similar low occupancy of jungle cat ($\psi = 0.247 \pm 0.020$) and leopard cat ($\psi = 0.178 \pm 0.019$) has been recorded in Parsa Koshi Complex (Sharma et al. 2024). In the central Indian reserve, the density of jungle cat was estimated as 4.01 (95% CI 2.65–6.12) individuals/100 km^2 (Chatterjee et al. 2020), and of leopard cats at Pakke tiger reserve was 3.2 individuals/100 km^2 by Selvan et al. (2014).

4.1 | Habitat Association and Detection Patterns

Both cats are recognized as habitat generalists, preferring habitats with adequate water and dense vegetation such as wetlands, reed beds, riparian areas, and grassland (Rostro-García et al. 2021; Miththapala et al. 2022; Pin et al. 2022), which align well with our findings where jungle cats were frequently detected in mixed sal and riverine forests near water sources. However, in a study conducted by Sharma et al. (2024), both cats were not influenced by the distance to water bodies. Though the proximity of water bodies may influence distributions of these species at a different spatial

TABLE 4 | Summary of the model-selection procedures for factors influencing the jungle cat's occupancy.

Models	*K*	AIC	ΔAIC	AICwt	cumltvWt
p (Habitat) ψ (TRI + Tiger + road)	8	889.79	0	9.80E-01	0.98
p (Habitat) ψ (road)	6	899.35	9.56	8.20E-03	0.99
p (Habitat) ψ (agb + settlement + TRI)	8	900.83	11.04	3.90E-03	0.99
p (Habitat) ψ (settlement + Tiger + agb)	8	901.07	11.28	3.50E-03	1
p (Habitat) ψ (Tiger + settlement)	7	904.3	14.51	7.00E-04	1
p (Habitat) ψ (agb)	6	904.86	15.07	5.20E-04	1
p (Habitat) ψ (Tiger)	6	906.55	16.76	2.30E-04	1
p (Habitat) ψ (TRI)	6	908.76	18.97	7.50E-05	1
p (Habitat) ψ (settlement)	6	916.43	26.64	1.60E-06	1
p (Habitat) ψ (.)	5	918.67	28.88	5.30E-07	1
p (Habitat) ψ (LC)	6	920.23	30.44	2.40E-07	1
p (Habitat) ψ (waterholes)	6	920.52	30.73	2.10E-07	1
p (Habitat) ψ (river)	6	920.63	30.84	2.00E-07	1

Note: AIC = Akaike information criterion, AICwt. = the AIC model weight, K = Number of model parameters including intercepts and covariates, ΔAIC = the difference in AIC values between each model and the model with the lowest AIC, ψ = the probability of habitat use, Tiger = Tiger index, settlement = Distance to the human settlement, CameraModel = Types of camera model used in the survey, road = Distance to road, river = Distance to river, Habitat = Types of habitat, TRI = Terrain Ruggedness Index, agb = Above Ground Biomass, LC = Occurrence of leopard cat.

TABLE 5 | Summary of the model selection procedures for factors influencing leopard cat occupancy.

Models	*K*	AIC	ΔAIC	AICwt	cumltvWt
p (waterholes) ψ (Habitat)	6	575.54	0	0.218	0.22
p (waterholes) ψ (Habitat + TRI)	7	575.63	0.093	0.208	0.43
p (waterholes) ψ (TRI)	4	575.99	0.447	0.174	0.6
p (waterholes) ψ (.)	3	577.91	2.368	0.067	0.67
p (waterholes) ψ (river)	4	578.36	2.824	0.053	0.72
p (waterholes) ψ (agb + settlement + TRI)	6	578.74	3.202	0.044	0.76
p (waterholes) ψ (Tiger)	4	578.85	3.306	0.042	0.81
p (waterholes) ψ (JC)	4	578.91	3.368	0.04	0.85
p (waterholes) ψ (agb)	4	578.91	3.371	0.04	0.89
p (waterholes) ψ (settlement)	4	579.43	3.888	0.031	0.92
p (waterholes) ψ (TRI + Tiger + agb)	6	579.76	4.22	0.026	0.94
p (waterholes) ψ (road)	4	579.91	4.367	0.025	0.97
p (waterholes) ψ (Tiger + settlement)	5	580.29	4.745	0.02	0.99
p (waterholes) ψ (settlement + Tiger + agb)	6	581.49	5.951	0.011	1

Note: AIC = Akaike information criterion, AICwt. = the AIC model weight, *K* = Number of model parameters including intercepts and covariates, ΔAIC = the difference in AIC values between each model and the model with the lowest AIC, ψ = the probability of habitat use, Tiger = Tiger index, settlement = Distance to the human settlement, Camera Model = Types of camera model used in the survey, road = Distance to road, river = Distance to river, Habitat = Types of habitat, TRI = Terrain Ruggedness Index, agb = Above Ground Biomass, JC = Occurrence of jungle cat.
Abbreviations: MF, Mixed Forest; RF, Riverine Forest; SF, Sal Forest; TG, Tall Grass.

resolution, as they serve as important resources for their prey species for hunting near the bed reeds of riverbanks and dry streams (Rostro-García et al. 2021). Also, our results showed differences in detection performance among camera models. Panthera camera traps consistently outperformed Cuddeback and Reconyx models in detecting both species. However, Shah et al. (2025) reported that for the detection of tigers, Reconyx was the best camera.

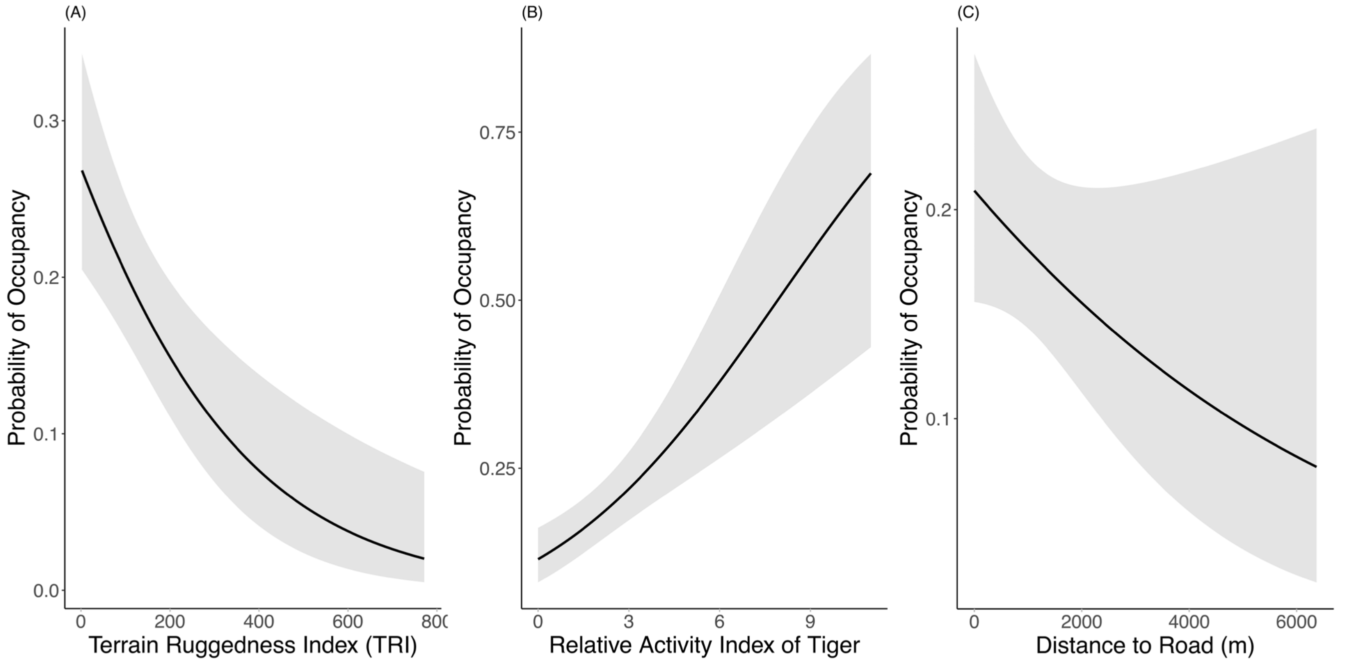

FIGURE 6 | Relationship between Terrain Ruggedness Index (TRI), occurrence of tiger, and distance to road (m) with probability of occurrence of jungle cat.

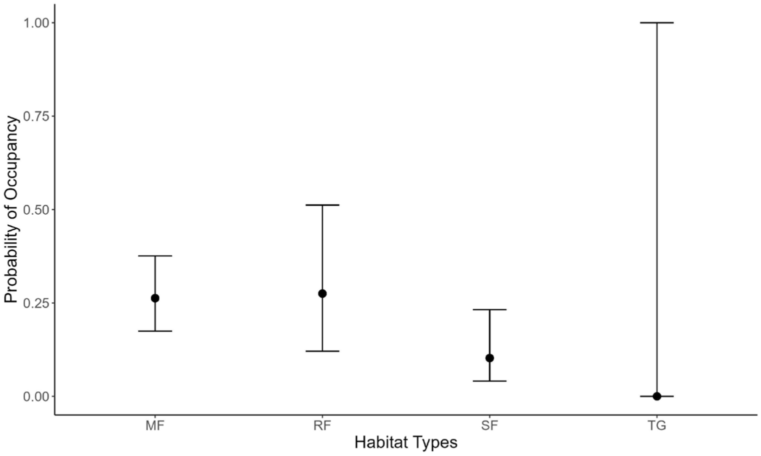

FIGURE 7 | Relationship between habitat types and probability of occupancy of the leopard cat.

4.2 | Occupancy Dynamics

At BNP, jungle cat occupancy was best explained by a combination of habitat, terrain ruggedness, tiger activity index, and distance to roads. The presence of large predators such as tigers and leopards can influence jungle cats within shared habitats (Lynam et al. 2013). The occupancy of jungle cats was positively influenced by the increasing tiger activity index, which aligns with the study of Sharma et al. (2024) in the Parsa–Koshi complex, with the possible reason being jungle cats scavenging on the kills of the larger predators (Wild Cat Conservation 2014). Though jungle cat and tiger shared the same landscape and indicated potential shared territories (Sunarto et al. 2015; Chatterjee et al. 2020; Thatte et al. 2020), there might be temporal avoidance between tiger and jungle cat to minimize the direct encounters (Karanth et al. 2017), which we could not conclude from our study. In the study, we observed that the occupancy of the jungle cats was reduced with the increase in the distance to roads. It has been reported that the jungle cats are vulnerable to roadkill because they tend to inhabit areas near roads (Shrestha et al. 2024), particularly in flatter lowland regions (Ashoori et al. 2024), therefore they might be avoiding it. As the east–west highway passes through the BNP, it poses a significant threat to wildlife because of habitat fragmentation and increased vehicle collisions (Shrestha et al. 2024; Thakur et al. 2025). In our study, jungle cat's occupancy was negatively correlated with TRI, which aligns with (Sunquist and Sunquist 2002) and (Duckworth et al. 2005) stating jungle cats prefer plains and lowlands, particularly areas with grasslands and wetlands. Chatterjee et al. (2020) also found jungle cats were negatively associated with forest cover and positively associated with open scrubland areas of the central Indian reserve.

Similarly, for the occupancy of the leopard cat, it was positively correlated with riverine habitats. This aligns with prior research

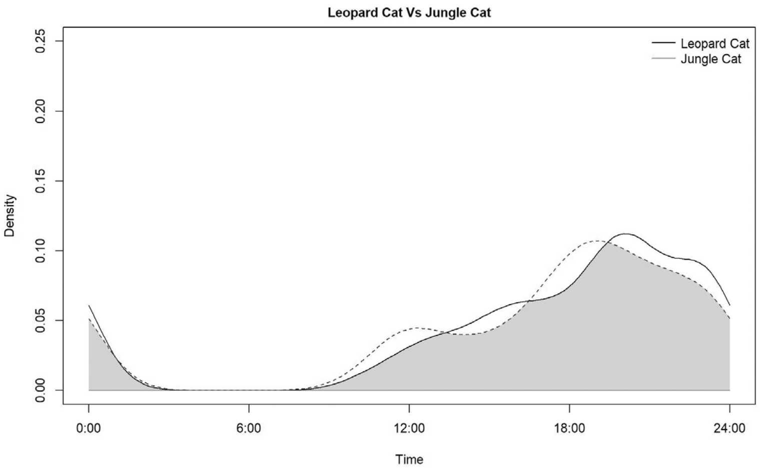

FIGURE 8 | Diel activity pattern of the sympatric jungle and leopard cat.

(Rho 2009; Lee et al. 2015; Lim et al. 2015; Luskin et al. 2023), which highlighted that leopard cats often inhabit riparian zones and inland wetlands. These areas provide essential resources, such as prey (small amphibians and reptiles) and dense vegetation for cover and refuge (Chung and Lee 2022). The occupancy of the leopard cat increased with the increasing TRI, which aligns with the study by Lim et al. (2015) stating it prefers steep slopes. These preferences can be justified as higher TRI landscapes provide numerous opportunities for concealment, natural escape routes, and diverse microhabitats, which are invaluable for hiding from larger predators and human disturbance (Wu et al. 2020; Ji et al. 2023). Jungle cats dominate open, riverine, and grassland habitats with high occupancy in fewer grids, while leopard cats dominate forested and semi-forested habitats with more evenly spread across BNP with moderate occupancy, indicating spatial segregation. Such spatial segregation has been recorded by Sharma et al. (2024), from the Parsa-Koshi complex of Nepal.

4.3 | Activity Overlaps and Temporal Partitioning

Our study observed that high activity overlaps between two species. Sharma et al. (2024) also recorded a high diel overlap (Dhat 1 = 0.802) between two species, and a similar result was observed in Cambodia by Rostro-García et al. (2021). Also, we concluded that the jungle cat is found to be predominantly nocturnal, which aligns with the study of Rostro-García et al. (2021). While previous reviews suggest that jungle cats tend to be more diurnal compared to other felids (Nowell and Jackson 1996; Sunquist and Sunquist 2002; Gray et al. 2014). Several empirical studies based on camera-trap and radio telemetry data, e.g., (Ikeda et al. 2016; Selvan et al. 2019; Mishra et al. 2020; Ünal and Eryilma 2020) have reported variable activity patterns ranging from diurnal to crepuscular and nocturnal, depending on prey availability and anthropogenic disturbance. Also, Sharma et al. (2024) reported that the jungle cat exhibited greater activity during early morning and evening.

Similarly, our study showed the nocturnal activity pattern of the leopard cat, which is consistent with several previous studies (Grassman et al. 2005; Lynam et al. 2013; McCarthy et al. 2015; Kamler et al. 2020), indicating the activity pattern of this felid is relatively consistent across its distribution. This nocturnal behavior of both small cats was not likely to avoid the larger carnivores because tigers and leopards are mostly nocturnal (Sunquist and Sunquist 2002) and, the jungle cat's occupancy was positively correlated with the presence of tigers in our case. A probable cause for both species being nocturnal is to avoid humans, like that observed in other species (Gaynor 2018). Also, the nocturnal habits of both species may be due to the abundance of their prey, which is mostly rodents, being nocturnal (Mukherjee et al. 2004). However, future research is needed to investigate whether activity patterns of both species are influenced by human activities.

5 | Conclusion

This study provides critical insights into habitat use and diel activity patterns of jungle cat and leopard cat in and around BNP, Nepal. The findings underscore the importance of maintaining a mosaic of riverine and sal forests, along with functional waterholes, for the conservation of small cats in BNP. Given the low occupancy and detectability of both species, conservation actions targeting small carnivores should be integrated into broader management strategies dominated by large carnivore conservation. To better understand the mechanism of distribution and niche partitioning between these sympatric felids, targeted diet studies are recommended. Diet information would clarify resource use and potential dietary overlap with each other and with larger predators, helping to distinguish whether spatial or trophic partitioning. The observed species-specific responses to environmental covariates emphasize the urgent need for tailored monitoring protocols, targeted conservation strategies, and enhanced public awareness campaigns to ensure the long-term survival of these crucial components of Nepal's biodiversity.

Author Contributions

Jyoti Sharma: conceptualization (lead), data curation (lead), formal analysis (lead), investigation (equal), methodology (lead), writing – original draft (lead), writing – review and editing (lead). **Narayan Prasad Gautam:** investigation (lead), methodology (equal), supervision (equal), validation (equal), writing – review and editing (equal). **Rabin Bahadur K. C.:** conceptualization (equal), data curation

(equal), formal analysis (equal), investigation (equal), methodology (equal), validation (equal), writing – original draft (equal), writing – review and editing (equal). **Morten Odden:** methodology (equal), writing – review and editing (equal). **Bed Kumar Dhakal:** methodology (equal), supervision (equal), writing – review and editing (equal). **Ajit Tumbahangphe:** methodology (equal), writing – review and editing (equal). **Naresh Subedi:** conceptualization (equal), funding acquisition (lead), methodology (equal), supervision (lead), validation (lead), writing – review and editing (equal).

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Ethics Statement

We obtained research permission from the Department of National Parks and Wildlife Conservation, Nepal (Ref number: 187-2081/2082, eco.: 1548; January 02, 2025). We did not carry out any experiments with live animals. Field surveys and data collection were conducted with prior approval from the department. We properly acknowledged supporting organizations for this research.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Upon publication of the article, all supporting data for obtaining the results have been made available via the Zenodo online data service. URL: https://doi.org/10.5281/zenodo.17167737.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **File S1:** Impact of covariates on probability of detection and occupancy for the jungle cats. **File S2:** Impact of covariates on probability of detection and occupancy for the leopard cats **File S3:** ece373305-sup-0001-FileS1-S4.zip. **File S4:** ece373305-sup-0001-FileS1-S4.zip.