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Factors associated with co-occurrence of fishing cat (*Prionailurus viverrinus*) with other carnivores.

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Abstract

Understanding how small-carnivores respond to the presence of other large and sympatric carnivores is critical to planning for multi-carnivore conservation programs. The fishing cat (*Prionailurus viverrinus)*, is sympatric to large mammalian carnivores across South Asia, yet its behavioural interactions with them remain poorly understood. In this study, we examined habitat use by fishing cats and their spatial and temporal overlap with other carnivores using camera-trap data. Occupancy modelling indicated that habitat variables, particularly the proportion of wetlands and grass–shrubland area, had higher relative variable importance. Fishing cats exhibited high spatial and temporal overlap with large carnivores such as tigers (*Panthera tigris*) and leopards (*P. pardus*). In contrast, spatial overlap with similar-sized felids (e.g., jungle cats, leopard cats, rusty-spotted cats) was comparatively lower, implying partial spatial segregation likely linked to dietary and habitat partitioning. Fishing cats were crepuscular–nocturnal during the cold-dry season but strictly nocturnal during the hot-dry season. Overall, our findings indicate that site use by fishing cats in our study area is likely to be mediated by habitat availability rather than by strong behavioural avoidance of large carnivores. Our results suggest that large-carnivore conservation may provide shared habitat protection for smaller carnivores such as fishing cats, but determining whether large carnivores exert effects on fishing cat populations will require long-term demographic and population-monitoring data. Conservation strategies for fishing cats should therefore prioritize maintaining wetland–grassland habitat mosaics, along with forests in floodplains to ensure that these wetland specialists persist alongside larger carnivores.

Introduction

Mammalian carnivores play important ecological role by regulating prey populations through predation and shape ecosystem functioning (Roemer et al., 2009). They are also among the most imperilled groups of species globally (Ripple et al., 2014). Conservation efforts for carnivores have often emphasized on large-bodied and charismatic species, such as tigers, snow leopards and jaguars, with the assumption that protecting these wide-ranging predators and their habitats will also benefit smaller sympatric species (Roberge and Angelstam, 2004; Thornton et al., 2016). Although such umbrella-species approaches can be valuable where habitat requirements overlap (Thapa, 2013; Deere et al., 2024), their effectiveness for conserving smaller or ecologically specialized species remains uncertain, particularly in landscapes that support diverse carnivore assemblages (Roberge & Angelstam, 2004; Sergio et al., 2008).

Carnivore communities are structured not only by shared habitat requirements but also by interspecific interactions (Holt and Pollis, 1997; Palomares & Caro, 1999). In a multi-carnivore system, interspecific interactions may affect how effectively such umbrella-species-focused conservation approaches benefit smaller/subordinate species. These interspecific interactions can be both positive and negative: Dominant predators may negatively influence smaller carnivores through interference competition, intraguild killing, or displacement from preferred habitats (Durant, 1998; Macdonald, 2004; Lamichhane et al., 2014; Vissia & Van Langevelde, 2022). Conversely, large carnivores may also generate indirect

benefits for subordinate species, for example, by providing scavenging opportunities or by suppressing other competitors (Chourasia et al., 2012; Prugh et al., 2020). Smaller carnivores may therefore respond to large carnivores in complex ways, including spatial segregation, temporal partitioning, habitat shifts, or continued co-occurrence where ecological niches differ sufficiently (Schoener, 1974). As a result, the presence of large carnivores does not necessarily indicate either facilitation or exclusion of smaller carnivores; instead, coexistence may depend on the relative importance of habitat features, resource availability, and interspecific effects operating at the scale of observation.

Assessing the relative influence of larger carnivores on small carnivores is particularly important for evaluating whether conservation strategies centred on large carnivores as “umbrella” species can also support smaller, subordinate, or habitat-specialist carnivores. One way to assess the viability of the umbrella species conservation approach is to determine whether smaller carnivores are more strongly influenced by habitat variables or interspecific interactions. If smaller carnivores are primarily associated with habitat variables that are also protected under large-carnivore conservation programs, then umbrella-based approaches may provide indirect conservation benefits. However, if their habitat use or activity patterns are more strongly shaped by the presence of dominant carnivores positively or negatively, then interspecific interactions may either constrain or modify these expected benefits. Understanding whether and how the role of habit availability and large carnivores play out in determining site use by smaller carnivores is therefore relevant in a multi-species planning context amid ongoing landscape changes that may alter both habitat availability and species interactions (Farris et al., 2020).

The fishing cat (*Prionailurus viverrinus)* provides a useful case for examining these questions. It is a medium-sized wetland-dependent felid with a patchy distribution across South and Southeast Asia and is classified as Vulnerable on the IUCN Red List (Mukherjee et al., 2016). Across parts of its range, it is known to co-occur with a diverse carnivore species, including tigers, leopards, jackals (*Canis aureus*), civets, and three small cats (Mishra et al., 2022; Petersen et al. 2022). Despite this sympatry, the species remains relatively understudied, and its behavioural ecology and interspecific interactions are also poorly known (Can et al., 2020; Mishra et al., 2020). Most existing research on small carnivores (Appel et al., 2013; Rai et al., 2018; Lama et al., 2019; Shrestha et al., 2020) is limited to their occurrence and distribution rather than their behavioural interactions with large carnivores. This limits our ability to determine whether conservation actions designed around larger carnivores and floodplain habitats are likely to safeguard wetland-specialist mesocarnivores.

In this study, we investigated factors associated with fishing cats' habitat use and their co-occurrence with sympatric carnivores in Shuklaphanta National Park, Nepal (Supplementary Table 1). Using multi-year camera-trap data, we assessed three complementary dimensions of coexistence: habitat use by fishing cats, spatial overlap with larger and smaller carnivores, and temporal activity overlap with sympatric carnivores. Specifically, we asked whether fishing cat habitat use was more strongly associated with habitat features, particularly wetland and grass–shrubland cover, or with the presence of larger and smaller carnivores.

We had two hypotheses: First, we hypothesized that fishing cats would spatially or temporally avoid dominant predators (tigers, leopards) and ecologically similar mesocarnivores (e.g., jungle cat (*Felis chaus*), civets (family Viverridae) to reduce predation risk (Palomares & Caro, 1999; Ritchie & Johnson, 2009), and competition (Wang et al. 2015) respectively. As such, we predicted limited spatial co-occurrence and temporal overlap between these species. Second, we hypothesized that habitat availability (Strampeli et al. 2023, Patel et al. 2023), would drive fishing cat occurrence, given their dependence on semi-aquatic habitat for prey and vegetative cover for hunting and shelter (Mukherjee et al., 2012; Mishra et al. 2018). We predicted that wetland area and grassland area would positively influence occurence of fishing cats.

Study area

The study was conducted in Shuklaphanta National Park (SNP) and adjoining forests in south-western Nepal (Fig. 1). The park is a part of the Terai Arc Landscape, a globally significant priority landscape for tiger conservation that connects several transboundary protected areas across Nepal and India (Chanchani et al., 2014). Shuklaphanta National Park encompasses approximately 305 km², surrounded by a 243.5 km² buffer zone (BZ). Elevation ranges from 175 to 1,300 m. The park is dominated by subtropical sal (*Shorea robusta*) forests interspersed with extensive alluvial grasslands and wetlands formed by the floodplains of the Mahakali and Chaudhar rivers. The resulting mosaic of ecological niches support a rich assemblage of 21 carnivores, including felids (5), canids (3), bear (1), hyaena (1) civets (4), mustilids (3) and mongooses (4) in SNP (Poudyal et al., 2020) (Supplementary Table 1).

The region has a subtropical monsoonal climate with three distinct seasons: a hot-dry season (March to mid-June), a monsoon season (mid-June to September), and a cold-dry season (October to February). The hot-dry season is characterized by high daytime temperatures exceeding 35°C and widespread drying of wetlands and grasslands, often accompanied by forest fires and intense human activity in peripheral areas. The monsoon brings heavy rainfall (1,500-2,000 mm annually) and extensive flooding along river valleys, rejuvenating grassland productivity. In contrast, the cold-dry season is cooler (10–25°C), with reduced human disturbance and stable water availability, providing optimal conditions for wildlife movement and camera-trap surveys.

Figure 1

Methods

Field survey

We adopted a systematic camera-trap design by overlaying a 2 × 2 km^2 grid cells across the study area. In each of these cells, we placed a pair of inward-facing not-baited cameras (Cuddeback C1, Panthera V5 & V6) at locations that maximize the chances of detecting the passing by animals. A minimum inter-trap distance of 1.5 km was maintained, and camera traps were placed across the gradients of habitat to

capture the variation in habitat features like grassland, wetland and forests. Camera traps were deployed at least 15 days at each locations across six consecutive years (2013–2018) in the cold-dry season (December to March). An additional survey was conducted in 2021 in the hot-dry season (April - June), resulting in a total of seven survey sessions (Supplementary Table 2). Across all surveys, ~ 100 cells across the SNP and BZ, totalling ~ 400 km^2, were consistently surveyed. In 2018, additional areas adjacent to the park were also surveyed as part of the national tiger survey, covering 252 grid cells (~ 1,000 km^2).

All photographs were systematically organized and labelled by species and camera trap-station identity. For analysis, consecutive photographs of the same species at a station were considered independent detections if separated by at least one hour (Mishra et al., 2021). The small Asian and Indian grey mongoose were combined into a single category because it was not always possible to distinguish them with certainty from camera trap images.

Habitat use

We used a single-species, single-season occupancy modelling framework to estimate the probability of site use by fishing cats while accounting for imperfect detection (MacKenzie et al., 2002; MacKenzie, 2006). The 15-day camera-trapping survey period was divided into three sampling occasions of five days each, providing the repeated detection–non-detection intervals required for single-season occupancy modelling. In this study, the camera sites were set for tiger surveys so the spacing exceeded the scale relevant to fishing cat home-range dynamics. Therefore, we suggest our estimates should be interpreted as reflecting habitat use rather than true occupancy.

Although camera-trapping data were collected over multiple years, we used only the 2018 dataset for the occupancy analysis because the single-season modelling framework requires demographic and geographic closure within a single sampling period, and pooling multi-year data would violate this assumption. The 2018 dataset was selected as it yielded the highest number of detections among recent surveys (2018 and 2021). Given the overall low detection rates (< 50 records), using a dataset with more detections enabled us to improve model performance and detect underlying patterns in species occurrence.

We used data from 198 camera traps from 99 grid cells across the national park (93 grid cells) and buffer zone (six grid cells). Data from outside the park and buffer zone were excluded from the analysis because no fishing cats were detected on the camera traps deployed there. Moreover, we needed to maintain the spatial consistency of different dimensions of analysis.

We considered four covariates expected to influence fishing cat habitat use, based on their known associations with wetland habitat, and expected interspecific interactions given their subordinate status (Mishra et al., 2018; Mishra et al., 2025a Mukherjee et al., 2012; Appel et al., 2013). (1) For the presence of large carnivores at a site (> 20kg), we created a binary variable indicating whether tigers or leopards

were detected in a given grid cell. (2) The presence of sympatric small carnivores was also represented as a binary variable indicating whether any other mesocarnivore (< 20 kg) was detected in the same grid cell.. (3) Amount of grassland-shrubland habitat within the grid cell was quantified as the proportion of each 2 × 2 km^2 grid cell covered by grassland and shrubland (hereafter grassland). (4) Likewise, we calculated the proportion of wetland and flooded vegetation within the grid cell. Land-cover classifications were extracted from the Government of Nepal's national Land Use and Land Cover dataset (published by the Department of Survey, Nepal, 30 × 30 m^2 resolution). We followed the standard procedure for fitting single-season occupancy models (MacKenzie et al., 2006). We fit multiple models based on ecologically informed combinations of occupancy covariates. Prior to model fitting, continuous variables were standardized (z-transformed), and collinearity among covariates was assessed. Grassland area and wetland area were strongly correlated and therefore never included in the same model. Because of this collinearity, a global model with all four covariates was not constructed. The final model set consisted of ten candidate models representing different combinations of habitat variables, large carnivore presence, and small carnivore presence.. Models were ranked using the Akaike information criterion (AIC) adjusted for small sample sizes (AICc; MacKenzie, 2006), with models having a ΔAICc < 2 considered strongly supported. We defined sample size as the number of grid cells surveyed. Additionally, we calculated the cumulative model weights by summing the Akaike weights of all models that included a given covariate to evaluate the relative contribution of that covariate to habitat use. The fit of the most general occupancy model was assessed for over-dispersion using a bootstrap goodness-of-fit test with 1,000 bootstrap samples (Burnham & Anderson, 2002).

Assessing patterns of temporal and spatial overlap

For the spatial overlap analysis, we included carnivore species with more than 10 independent detections in the 2018 cold-dry season survey and the 2021 hot-dry season survey. These two survey periods were selected because they provided the most consistent spatial sampling for comparing species co-detections across camera-trap stations. For the temporal overlap analysis, however, we used all available detections from the 2013–2018 and 2021 surveys. Unlike spatial overlap and occupancy analyses, which are sensitive to differences in the spatial arrangement of sampling units, temporal activity analyses are based on the timing of independent detections and are therefore less likely to be affected by spatial inconsistencies among survey years. For temporal overlap analysis, we classified detections from the 2013–2018 surveys as representing the cold-dry season and detections from the 2021 survey as representing the hot-dry season, based on the timing of camera deployment.

Pairwise spatial overlap was measured using the Sørensen similarity index (Sorensen, 1948; Torretta et al., 2016):

$$Ssi,j=2aij/(2aij + bij+cij)$$

Where, aij represents the number of grid cells where both species i and j were present, and b ij and c ij are the number of grid cells where only one species was present. This index ranges from 0 (maximum

segregation) to 1 (maximum co-occurrence, i.e., both species co-occur in all cells they are detected).

To examine habitat associations, each camera-trap station that detected a fishing cat was assigned to one of three dominant habitat types (grassland, forest, or wetland) based on standard land-use/land-cover classifications. This allowed us to evaluate whether the spatial detection patterns of fishing cats reflected their known habitat preferences and whether overlap with other carnivores varied across habitat types.

Diel activity patterns and temporal overlap was estimated using non-parametric kernel density functions implemented in the 'overlap' package in R (R Core Team, 2020).

Results

Survey summary

Across seven surveys in Shuklaphanta National Park and its adjoining forests, a total survey effort amounted to 13,576 camera trap days with an average of 1,939 (1,206–4,604) trap days per survey. The survey effort was higher in the cold-dry season (11,848 trap days) compared to the hot-dry season (1,728 trap days) (Supplementary Table 2). In total, we recorded 3,899 independent detections of 22 carnivore species across the surveys (Table 1), with 350 detections of 12 species in the hot-dry season and 3,549 detections of 22 species in the cold-dry season. The total number of species detected varied across years. For example, in the 2021 survey, we detected 12 carnivore species compared to 17 species detected in 2018 (Table 1). Golden jackal had the highest detections (n = 1,173) followed by tiger (n = 619), common leopard (n = 517), small Indian civet (n = 247), and fishing cat (n = 147).

Table 1

Summary of different carnivore species detections in camera trapping and detection rate (detections per 100 trap days) in various years in the Shuklaphanta National Park area, Nepal arranged in ascending order of their body size. A detection event of the same species at the same station is considered independent if two detections were at least an hour apart. The species in bold have 10 or more detections and thus included in spatial and temporal analysis.

SN	Species	No. of independent detections & detection rate in parenthesis							Total for cold-dry season
		2013	2014	2015	2016	2017	2018	2021	(2013–2018)
1	**Small Asian/Indian grey mongoose**	19 (1.45)	8 (0.66)	11 (0.83)	14 (0.71)	18 (1.25)	56 (1.22)	8 (0.46)	126
2	**Rusty-spotted cat**	9 (0.69)	2 (0.17)	2 (0.15)	9 (0.46)	3 (0.21)	20 (0.43)	2 (0.12)	45
3	**Ruddy mongoose**	9 (0.69)	0	0	1 (0.05)	0	1 (0.02)	8 (0.46)	11
4	Crab eating mongoose	0		0	2 (0.1)	0	1 (0.02)	0	3
5	Yellow-throated marten	0	0	0	0	0	8 (0.17)	0	8
6	**Bengal fox**	5 (0.38)	8 (0.66)	5 (0.38)	7 (0.36)	53 (3.68)	29 (0.63)	15 (0.87)	107
7	**Leopard cat**	0	0	0	10 (0.51)	5 (0.35)	65 (1.41)	0	80
8	**Small Indian civet**	42 (3.21)	25 (2.07)	25 (1.89)	52 (2.65)	25 (1.73)	61 (1.32)	17 (0.98)	230
9	**Common palm civet**	11 (0.84)	15 (1.24)	5 (0.38)	36 (1.83)	6 (0.42)	35 (0.76)	9 (0.52)	108
10	**Masked palm civet**	0	2 (0.17)	0	0	0	19 (0.41)	0	21
11	**Jungle cat**	11 (0.84)	8 (0.66)	14 (1.06)	18 (0.92)	34 (2.36)	50 (1.09)	4 (0.23)	135
12	**Fishing cat**	14 (1.07)	17 (1.41)	29 (2.19)	22 (1.12)	26 (1.8)	25 (0.54)	14 (0.81)	133

SN	Species	No. of independent detections & detection rate in parenthesis							Total for cold-dry season (2013–2018)
		2013	2014	2015	2016	2017	2018	2021	
13	**Honey badger**	13 (0.99)	3 (0.25)	21 (1.59)	13 (0.66)	26 (1.8)	35 (0.76)	23 (1.33)	111
14	Smooth-coated otter	0	0	6 (0.45)	1 (0.05)	6 (0.42)	0	0	13
15	Large Indian civet	0	0	0	0	0	2 (0.04)	0	2
16	**Golden jackal**	31 (2.37)	32 (2.65)	76 (5.74)	74 (3.77)	218 (15.13)	700 (15.2)	42 (2.43)	1,131
18	Striped hyena	4 (0.31)	0	0	0	2 (0.14)	0	0	6
19	**Common leopard**	46 (3.51)	27 (2.24)	56 (4.23)	79 (4.02)	67 (4.65)	104 (2.26)	138 (7.99)	379
20	Sloth bear	1 (0.08)	0	0	0	0	0	0	1
21	**Tiger**	72 (5.5)	68 (5.64)	88 (6.65)	123 (6.26)	108 (7.49)	90 (1.95)	70 (4.05)	549
Total		288	215	338	461	597	1,301	350	3,549

Table 1

Fishing cat habitat use

The estimated probability of fishing cat habitat use was 0.29 (SE = 0.10), indicating that fishing cats used nearly one third of surveyed grid cells after accounting for imperfect detection. The top two highest-ranked models included grassland area and small carnivore presence, suggesting that these variables contributed to relatively better model fit within the candidate set (Table 2). Consistent with this pattern, grassland area had the highest relative variable importance (0.94), followed by small carnivore presence (0.43), in explaining variation in fishing cat habitat use (Table 3). However, coefficient estimates for all examined covariates were non-significant ($p > 0.05$, Table 3) and their confidence intervals overlapped zero, indicating limited support for strong individual effects.

Table 2

Single season occupancy models describing the occurrence of the fishing cat in Shuklapanta National Park, Nepal during February 2018, ranked according to the Akaike information criterion adjusted for small sample size (AICc).

Model*	***K*#**	**AICc**	**ΔAICc[à]**	**loglink**	$W_i^{£}$
Psi (Small carnivore+grassland) p(.)	4	147.44	0.00	−69.51	0.42
Psi(grassland) p(.)	3	147.77	0.33	−70.76	0.36
Psi(Large.carnivore+grassland) p(.)	4	149.39	1.94	−70.48	0.16
Psi(.) p(.)	2	153.98	6.54	−74.93	0.02
Psi(large carnivore) p(.)	3	154.56	7.12	−74.16	0.01
Psi(small carnivore) p(.)	3	154.88	7.44	−74.31	0.01
Psi(large carnivore+small carnivore) p(.)	4	155.06	7.62	−73.32	0.01
Psi(wetland cover) p(.)	3	156.10	8.66	−74.92	0.01
Psi(large carnivore+wetland) p(.)	4	156.66	9.22	−74.12	0.00
Psi(small carnivore+wetland) p(.)	4	157.05	9.61	−74.31	0.00

*Large carnivore, presence (1) or absence (0) at the camera trap station; Small carnivore, presence (1) or absence (0) at the camera trap station; Grassland, area of grassland and shrubland mixed habitat area in square kilometer within 2×2 sq.km grid cells; Wetland, area of wetland and flooded vegetation combined in square kilometers within 2×2 sq.km grid cells. Psi () represents the occupancy probability component of the mode, whereas p () represents the detection probability sub-model. #Number of parameters.

[à]Difference between the AICc value of the best-supported model and successive models.

[£]Akaike model weight.

Table 3
Conditional model-averaged parameter estimates and 95% confidence interval of covariates explaining the occupancy of fishing cats in Suklaphanta National Park, Nepal, during February 2018.

Parameter	Average estimate	SE	Confidence interval	*z*	*p*	Relative variable importance[£]
Large carnivore presence/absence	1.39	1.40	−1.35–4.13	0.99	0.32	0.18
Small carnivore presence/absence	−2.95	2.52	−7.89–1.99	1.17	0.24	0.43
Area of grassland-shrubland in grid	5.45	3.98	−2.35–13.25	1.37	0.17	0.94
Area of wetland in grid	−0.04	0.35	−0.73 – 0.65	0.13	0.89	0.01

[£] Relative importance of a variable was calculated as the sum of Akaike weights for models containing the parameter, divided by the total sum of Akaike weights

Table 2

Table 3

Figure 2

Spatial overlap of carnivores

Spatial overlap between fishing cats and other species varied across two seasons (Table 4, Supplementary Table 4). In the cold-dry season of 2018, fishing cats had the highest spatial overlap with tigers (0.43), followed common leopards (0.21) and Small Asian/Indian grey mongoose (0.18). In contrast, during the 2021 hot-dry season, the fishing cat had the highest overlap with the Ruddy mongoose (.31), followed by tiger (0.29) and common leopard (0.21) (Table 4).

Table 4
Co-occurrence of fishing cats with other carnivore species at camera-trap stations, expressed as Sørensen similarity indices (SSI) during the cold-dry season (2018 Dec-Mar) and hot-dry season (2021, Apr-June) in Shuklaphanta National Park, Nepal. (For more details, refer to Supplementary file S1.)

Species name	**Spatial overlap index**	
	Cold-dry season	**Hot-dry season**
Small Asian/Indian grey mongoose	0.18	0
Rusty-spotted cat	0	0
Ruddy mongoose	0	0.31
Bengal fox	0	0
Leopard cat	0	ND*
Small Indian civet	0.12	0.1
Common palm civet	0.07	0
Masked palm civet	0	ND*
Jungle cat	0.06	0
Honey badger	0	0.21
Golden jackal	0.11	0.08
Common leopard	0.21	0.21
Tiger	0.43	0.29
*ND – Not Detected		

Table 4

Figure 3

Activity overlap of fishing cats with other carnivores

Fishing cats exhibited distinct diel activity patterns between seasons (Fig. 4). During the cold-dry period, (2013–2018), fishing cats showed a crepuscular–nocturnal pattern, with activity peaks shortly after sunset and again before dawn. In contrast, during the hot-dry season in 2021, fishing cats were strictly nocturnal (Fig. 2). Among the species that spatially overlapped with fishing cats in the cold-dry season, all but the mongoose (small Asian / Indian grey) showed nocturnal or crepuscular activity pattern (Fig. 4a). In the hot-dry season, most of species exhibited predominantly nocturnal or crepuscular activity patterns (4b).

The degree of temporal overlap of fishing cats with other carnivores varied across seasons. In general, higher overlap was observed during the cold, dry season, when overall carnivore activity became more nocturnal than in the hot, dry season (Table 5). The greatest overlap occurred with tigers (Δ = 0.86 [0.85–0.94]) and leopards (Δ = 0.82 [0.75–0.89]), followed by jungle cats, golden jackals, and small Indian civets (Δ = 0.73–0.80) during cold dry season. Across both seasons, fishing cats exhibited moderate to high temporal overlap (Δ > 0.70) with most nocturnal and crepuscular carnivores and low overlap (Δ < 0.40) with diurnal species (Table 2). Pairwise activity overlap values among all carnivore species are presented in Supplementary Table 3.

Table 5

Temporal activity overlap estimates (Δ) with 95% confidence intervals between fishing cats (*Prionailurus viverrinus*) and other sympatric carnivores recorded in camera-trap surveys in the cool-dry season (2013–2018) and hot-dry season (2021) in Shuklaphanta National Park, Nepal. Values represent temporal overlap coefficients between diel activity patterns of fishing cats and each carnivore species. “NA” indicates that a species was not detected or did not spatially overlap with fishing cats in that season.

Species overlapping with fishing cat	Cold-dry season Δ (95% CI)	Hot-dry season Δ (95% CI)
Mongoose (small Asian / Indian grey)	0.34 (0.19–0.35)	0.21 (0.04–0.75)
Rusty-spotted cat	0.74 (0.71–0.88)	NA
Ruddy mongoose	0.83 (0.79–1.0)	0.11 (0.01–0.72)
Bengal fox	0.69 (0.56–0.79)	0.47 (0.30–0.77)
Leopard cat	0.75 (0.68–0.85)	NA
Small Indian civet	0.77 (0.72–0.86)	0.56 (0.33–0.82)
Common palm civet	0.75 (0.64–0.84)	0.65 (0.59–0.93)
Masked palm civet	0.69 (0.52–0.83)	NA
Jungle cat	0.80 (0.72–0.90)	NA
Honey badger	0.73 (0.61–0.82)	0.63 (0.43–0.86)
Smooth-coated otter	0.50 (0.29–0.73)	NA
Golden jackal	0.77 (0.66–0.83)	0.51 (0.31–0.71)
Common leopard	0.82 (0.75–0.89)	0.65 (0.52–0.85)
Tiger	0.86 (0.85–0.94)	0.69 (0.62–0.91)

Table 5

Figure 4

Discussion

We investigated whether presence of large carnivore and other sympatric carnivores, and habitat availability influence the site use by fishing cats, alongside the extent of temporal and spatial overlap between them. Overall, our findings suggest that fishing cats persist within a multi-carnivore assemblage likely through habitat association and ecological specialization, rather than through strong spatial or temporal avoidance of larger carnivores and other sympatric carnivores.

Habitat availability appeared to be the most consistent correlate of fishing cat's site use in our study. The top-ranked occupancy models included grassland area, which had the highest relative importance among the covariates examined (Table 3). Although individual coefficient estimates were not statistically significant, the direction and relative support of the models are consistent with the known ecology of fishing cats as wetland-associated felids that use dense vegetation, floodplain edges, and grass–shrub mosaics for movement, concealment, and foraging (Mishra et al. 2018; 2025a; Petersen et al. 2023). In Shuklaphanta, these habitat features occur within a heterogeneous floodplain mosaics of wetlands, river channels, grasslands, and forest edges. An extensive intact grasslands (~ 35 km²) interspersed with wetlands along the Mahakali and Chaudhar River floodplains likely provide ideal habitat conditions for fishing cats in Suklaphanta (Poudyal et al., 2020). Such habitat heterogeneity may provide both aquatic and semi-aquatic prey resources and structural cover, allowing fishing cats to use areas that are also occupied by other carnivores while reducing direct encounters at finer spatial scales.

The apparent importance of grassland habitat should therefore be interpreted within the broader floodplain context of the species' ecology (Chauhan and Gopal, 2005). Grass cover may not simply represent terrestrial vegetation, but may also index the structurally complex wetland margins and floodplain ecotones used by fishing cats (Mishra et al. 2022). These areas likely provide a combination of hunting substrate, refuge, and movement corridors (Mukherjee et al. 2012; Mishra et al. 2022). The lack of strong statistical significance in the occupancy models does not necessarily negate the ecological relevance of these habitat variables; rather, it suggests that the available data were insufficient to estimate their effects precisely. This is plausible given the relatively low number of fishing cat detections and the fact that the camera-trap grid was originally designed for larger carnivores. Fine-scale features such as marsh edges, shallow wetlands, water depth, prey availability, and local human disturbance at fine spatial scale may be more relevant to fishing cat habitat use than the broader 2 × 2 km grid cell-level covariates available for this analysis.

Fishing cats showed considerable spatial and temporal overlap with large carnivores, particularly tigers and leopards. This finding does not support a strong pattern of broad-scale avoidance of dominant carnivores by smaller carnivores. Elsewhere, smaller carnivores have been found to avoid large carnivores (Allen et al. 2024). In our study context, the observed overlap should not be interpreted as evidence that large carnivores directly facilitate fishing cats. A more cautious interpretation is that fishing cats and large carnivores may share portions of the same landscape because they may be responding to overlapping environmental features, such as low-disturbance highly productive floodplain habitats, water availability, prey-rich areas, and movement corridors. In this sense, the positive association between fishing cat habitat use and large carnivore presence may reflect selection for

similar environmental features (Strampelli et al. 2023; Blanchet et al. 2020) rather than a direct ecological benefit from large carnivores.

This interpretation has important implications for the umbrella-species assumption often associated with large-carnivore conservation. The co-occurrence of fishing cats with tigers and leopards suggests that protected landscapes managed for large carnivores can include habitat conditions suitable for smaller wetland specialists. However, the benefit of such conservation is likely conditional on whether large-carnivore conservation also maintains the fine-scale habitat features required by fishing cats (Mishra et al. 20025). Tiger-focused protection may help safeguard broad floodplain landscapes from conversion and disturbance (Thapa, 2013), but it will not necessarily conserve fishing cats if wetlands, marsh edges, grass–shrub mosaics, and riparian microhabitats are degraded or overlooked. Thus, our results provide cautious support for the potential value of large-carnivore conservation landscapes for fishing cats, while also emphasizing that umbrella effects depend on habitat overlap and habitat quality rather than on the presence of large carnivores alone.

In contrast to the overlap observed with large carnivores, fishing cats showed lower spatial overlap with several medium- and small-sized carnivores, including ecologically similar felids (Table 4). This pattern may indicate partial spatial segregation among species with more similar body sizes, prey bases, or habitat requirements. Fishing cats, jungle cats, leopard cats, rusty-spotted cats, civets, mongooses, and jackals may all use overlapping portions of the floodplain landscape, but they are unlikely to use all habitat components in the same way. Fishing cats are more strongly tied to wetlands and floodplain margins (Mukherjee et al. 2012; Mishra et al. 2022), whereas some sympatric small carnivores may use drier grassland, forest edge, or more terrestrial habitats (Chatterjee et al. 2020; Rostro-García et al. 2021). Such habitat partitioning could reduce competition without requiring strong temporal avoidance.

The relationship with small carnivores was also reflected in the occupancy analysis, where small carnivore presence appeared in the top-ranked model and had the second-highest relative variable importance, although its coefficient was statistically insignificant (Tables 2 and 3). This suggests that small carnivore occurrence may be a relevant correlate of fishing cat habitat use, but the direction and strength of this association remain uncertain. A negative association, if supported by additional data, could reflect competition, habitat partitioning, or differences in microhabitat preference. Alternatively, it could arise from sampling effects if camera placement favoured certain movement routes or habitat types used more frequently by some species than by fishing cats. Therefore, rather than concluding that small carnivores suppress fishing cat habitat use, our results are better interpreted as indicating that interactions or habitat partitioning among similarly sized carnivores warrant closer investigation.

The temporal overlap results further suggest that the coexistence of sympatric carnivores in this system is not primarily structured by strict temporal segregation. Fishing cats were largely crepuscular to nocturnal in the cold-dry season and shifted toward more strictly nocturnal activity in the hot-dry season. Many sympatric carnivores, including tigers, leopards, jungle cats, jackals, civets, and other nocturnal or crepuscular species, also exhibit activity peaks at night. Consequently, fishing cats often overlapped

temporally with both larger and smaller carnivores. This pattern suggests that temporal avoidance is not the dominant mechanism separating species in this landscape. Instead, multiple carnivore species may co-occur in heterogeneous floodplain-grassland habitats by partitioning niches based on diet. Unlike large carnivores like tigers and other sympatric species such as jungle cats, fishing cats generally target smaller prey, including fish, amphibians, birds, and rodents (Mishra et al., 2018, 2021). Such prey-partitioning may also allow these species to coexist, as documented in other multi-carnivore systems (Muller et al. 2022). Overall, these results across dimensions (site use, spatial overlap, and temporal overlap) suggest that fishing cat coexistence with other carnivores in Shuklaphanta is likely mediated more by habitat availability than by broad-scale avoidance in distribution or strong behavioural avoidance at fine scale.

Several limitations should be considered when interpreting these results. First, the camera-trap design was developed primarily for tiger monitoring, and the 2 × 2 km grid scale may be too coarse to capture fine-scale habitat selection by fishing cats. Second, the number of fishing cat detections was relatively low, reducing statistical power and contributing to imprecise occupancy-model estimates. Third, the available habitat covariates were broad land-cover measures and did not directly quantify key ecological variables such as wetland depth, seasonal water persistence, and aquatic prey abundance. Fourth, spatial and temporal overlap metrics describe patterns of co-occurrence, but they do not directly identify the behavioural mechanisms underlying those patterns. Future studies should therefore combine finer-scale camera trap studies with fine-scale habitat variables, and, where possible, telemetry or genetic diet analysis to test whether observed overlap in space and time reflects shared habitat preference, resource partitioning, avoidance, or competition.

Our findings have direct conservation implications for fishing cats and other small carnivores in tiger-dominated low grassland-floodplain landscapes. Conservation strategies focused on large carnivores may benefit fishing cats where they protect intact floodplain systems, reduce habitat conversion, and maintain low-disturbance wetland–grassland mosaics. However, fishing cat conservation cannot rely solely on broad tiger-centred protection. The persistence of this wetland specialist depends on maintaining fine-scale habitat elements, including wetlands, marshes, riparian corridors, and grass–shrub ecotones. Management should therefore explicitly incorporate wetland protection, restoration of degraded floodplain habitats, seasonal water management, and disturbance reduction near key wetland areas. Such actions would strengthen the conservation value of large protected areas for the broader carnivore community while ensuring that smaller and more specialized carnivores are not overlooked within multi-species conservation planning.

Declarations

Author contributions

Study design and fieldwork: RM, BRL, NS, KT, BRD, HHI; data analysis: BRL, RM, GK; writing, review and editing: all authors.

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Conflicts of interest

None.

Ethical standards

The study was based on non-invasive camera trapping survey. All necessary permits for the study was obtained from the Department of National Parks and Wildlife Conservation, Nepal. The article abides with the Oryx's ethical standards.

Data availability

Data and supporting information related to this paper will be made available on request to corresponding authors.

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Figures

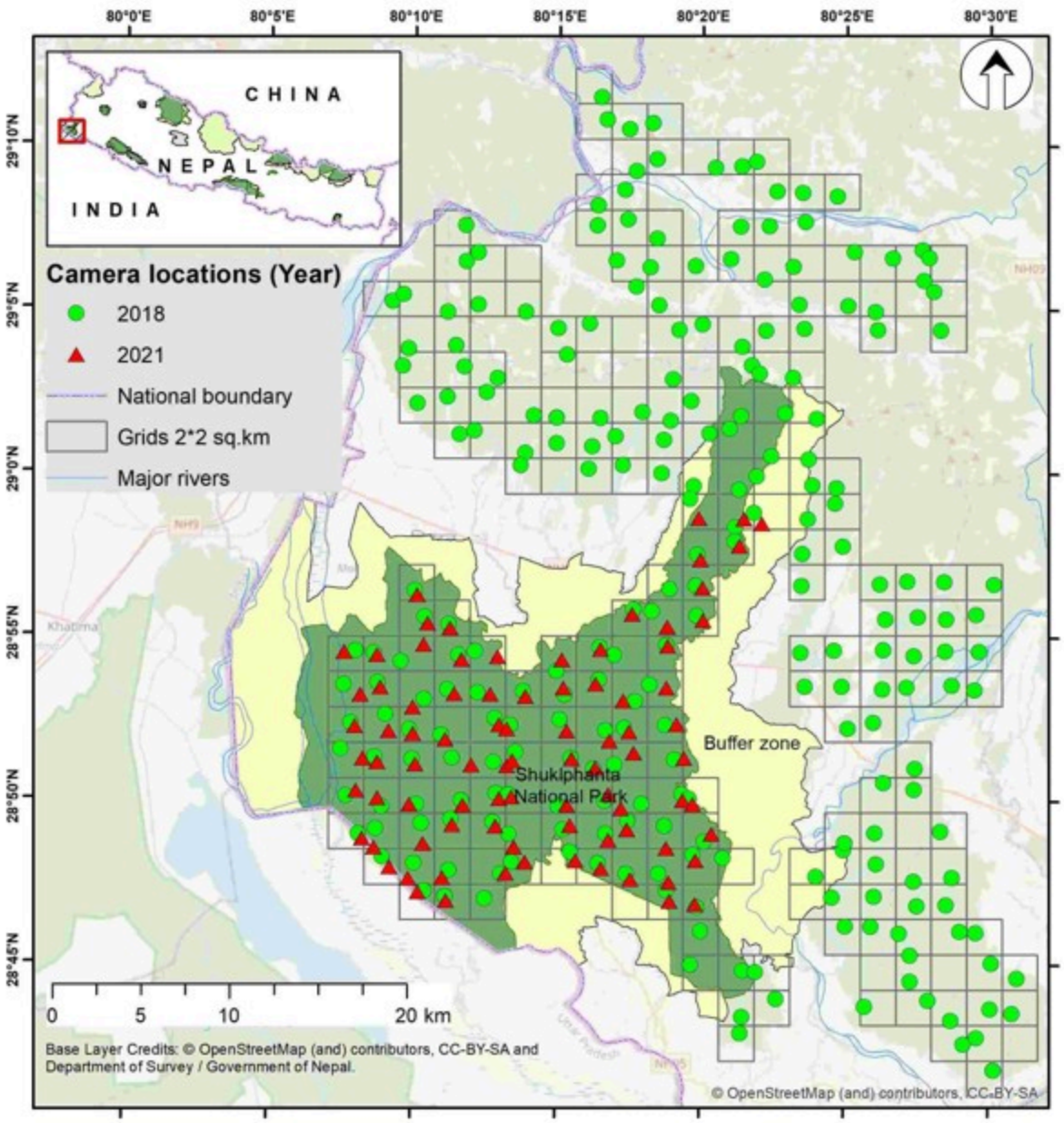


Figure 1

Camera trap locations inShuklaphanta National Park and adjoining forest area of the years 2018 and 2021. The camera trap coverage of 2013 – 2017 is similar to that of 2021, and therefore not shown differently in the map.

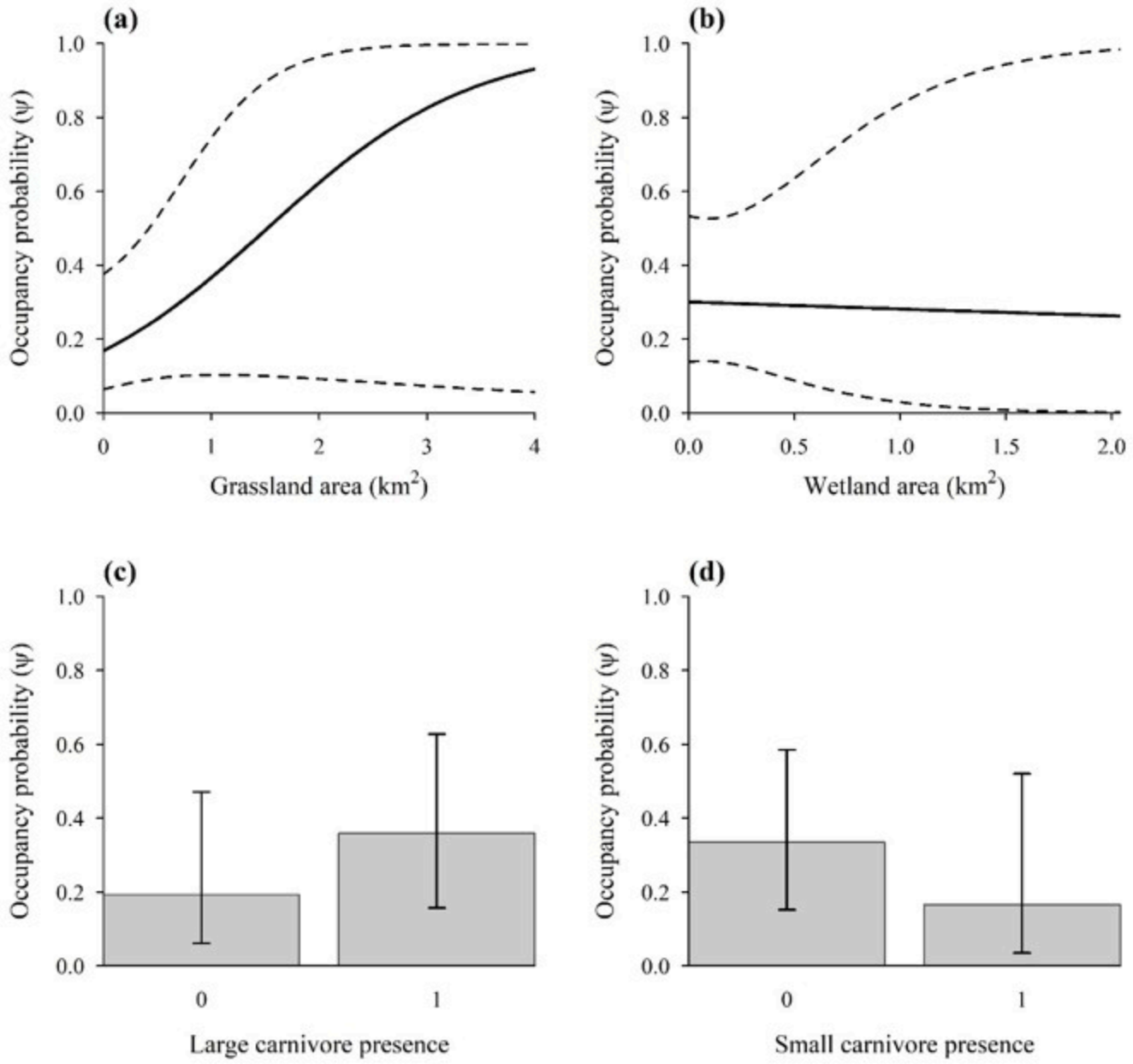


Figure 2

Predicted relationships based on model-averaged relationships between fishing cat habitat use and the examined covariates with uncertainty intervals a) area (km2) of grassland-shrubland, b) area of wetland, c) presence/absence (1/0) of large carnivores, d) presence/absence (1/0) of small carnivores in survey grid cells (2×2 km2).

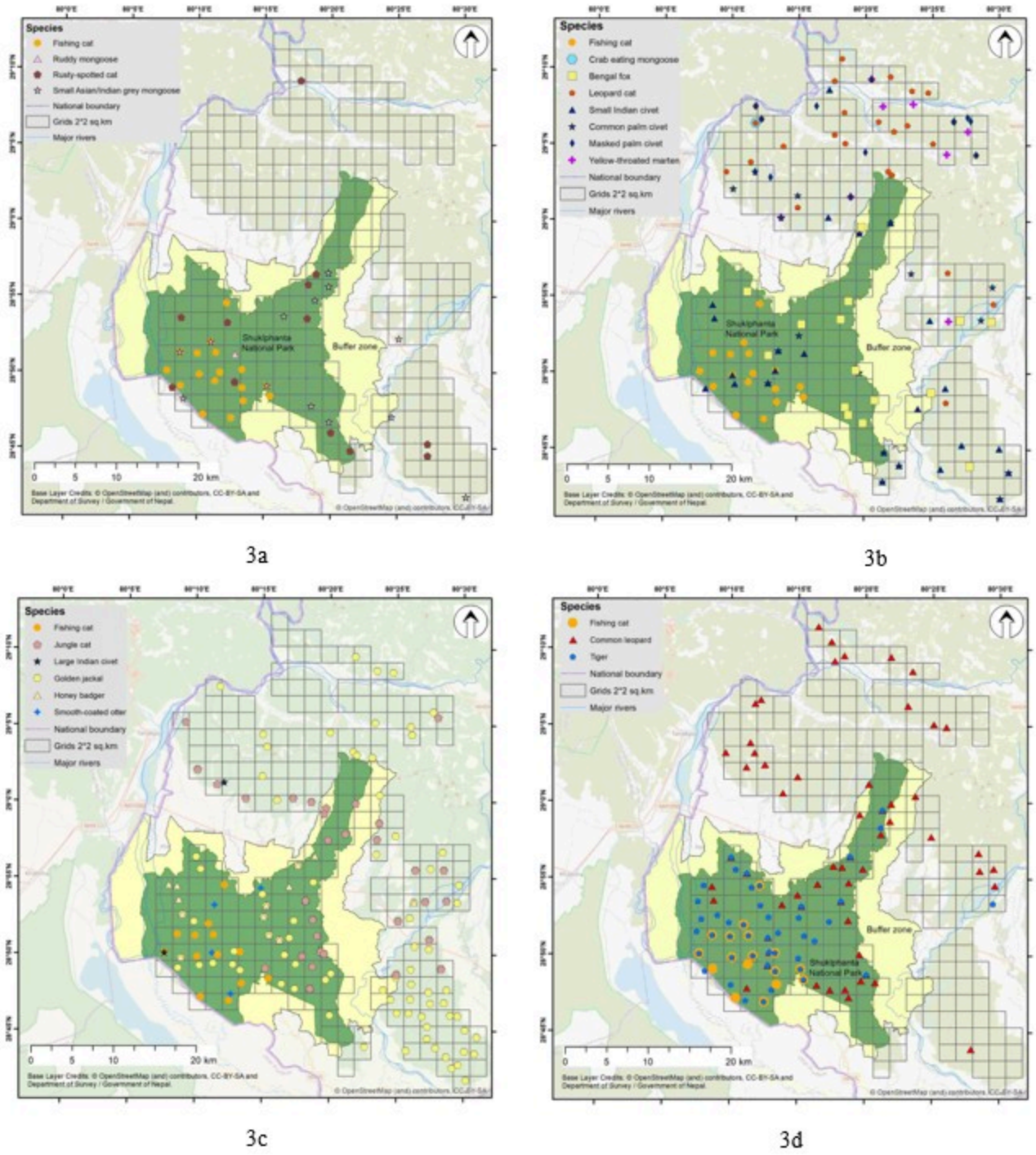
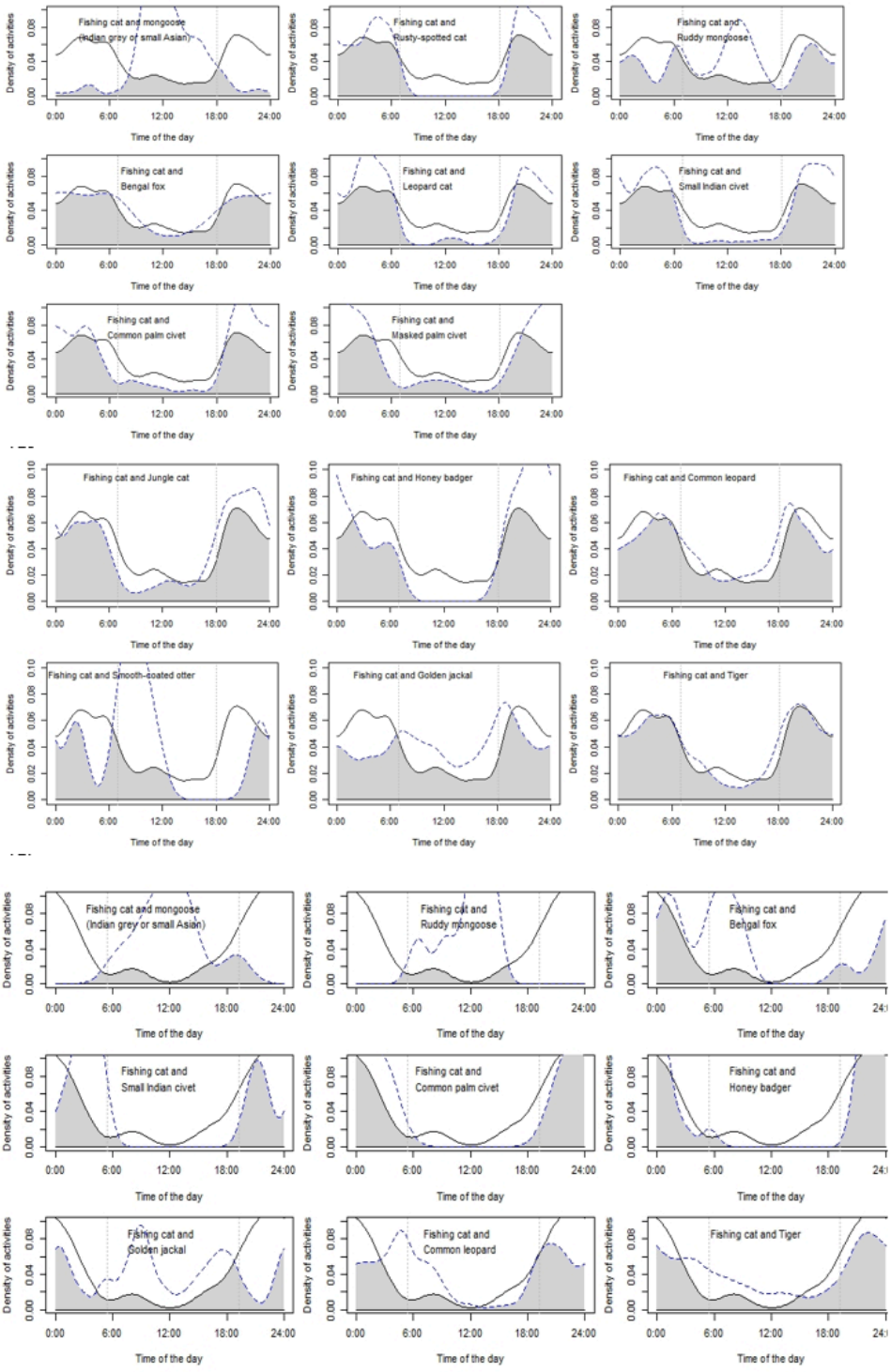


Figure 3

Carnivores distribution in Shuklaphanta National Park and adjoining forest based on 2018 camera trapping. Where 3a, 3b, 3c, and 3d represents distribution of carnivores < 2kg, 2-5 kg, 5-10 kg and Mega carnivores respectively (Note: Distribution of smooth-coated otter in Fig. 3c was based on their record in 2015, 2016 and 2017).



(b)

Figure 4

Temporal activity of fishing cats and other carnivores in cold-dry season (a), and hot-dry season (b). Continious and dotted lines represents the activity pattern of fishing cat and other carnivore respectively; and the shaded part is overlap between them.

Supplementary Files

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