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ORIGINAL ARTICLE

Spatio-temporal overlap of leopard and prey species in the foothills of Shiwalik, Himalaya

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Abstract
Understanding the interspecific interactions (spatial and temporal) between predators and their prey species is important to understanding the prey preferences for conservation and management decisions. However, due to large predators' wide-ranging, nocturnal, and cryptic behaviour, it is often difficult to assess their interactions with prey species. Therefore, we determined the spatial and temporal interactions of leopard (*Panthera pardus*) with potential prey species in Kalesar National Park (KNP) using camera traps from January 2020 to April 2020. KNP is situated in the foothills of the Shiwalik mountain range of Himalaya, North India. We used encounter rates and activity patterns to understand the spatial and temporal overlap between leopards and prey species. We used composite scores to predict the potential prey preferences using the photo-capture data. A total sampling effort of 1150 trap nights documented 92 photo-captures of leopards with a detection rate of 17.3 leopards per 100/trap nights. Leopards exhibited bimodal peaks and were active throughout the day and night but showed more diurnal activity. Leopards had the highest temporal overlap with chital (*Axis axis*) and wild boar (*Sus scrofa*) and the highest spatial overlap with wild boar, peafowl (*Pavo cristatus*), and sambar (*Rusa unicolor*). Due to their high composite scores, wild boar, sambar, peafowl, and chital were predicted the most preferred prey species for leopards. Our results suggest that effective management of preferred prey species in the area is required to ensure the conservation of the leopard population.

Keywords Activity pattern · Camera trap · Himalayas · Kalesar National Park · *Panthera pardus* · Prey preference · Interspecific competition

Introduction

Interactions between predator and prey are an important component of community ecology to understand the functioning of the ecosystem and explore the ecological niches occupied by species (Allen et al. 2021; Havmøller et al. 2020a, b). Moreover, the spatial and temporal overlap between predator and prey indicates prey preferences (Fortin et al. 2015; Allen et al. 2021). Depending upon the preferred prey species' body size and morphological adaptations, predators synchronize their daily activities spatially and temporally (Ramesh et al. 2015; De Matos et al. 2018). The leopard (*Panthera pardus*) is a small-bodied predator with an average weight of 63 kg (range 45–75 kg; Athreya and Belsare 2008). Leopards overlap their activities with medium- to small-bodied prey species such as chital (*Axis axis*), barking deer (*Muntiacus muntjac*), and wild boar (*Sus scrofa*) (Karanth and Sunquist 1995; Mondal et al. 2011; Harihar et al. 2011). It is classified as 'vulnerable' throughout its distributional range, but several subspecies are endangered, and the species is in overall decline; the latest genetic study indicates that African and Asian leopards are two species and thus makes Asian even more threatened than currently classified (Jacobson et al. 2016; Stein et al. 2020). It is a widely distributed cat and adaptive to survive in various ecosystems (Jacobson et al. 2016). However, their cryptic behaviour and low abundance make it difficult to study the interspecific interactions in their guild and prey species (Ripple et al. 2014; Havmøller et al. 2020a, b). The

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development of camera traps has advanced the study of cryptic mammals' ecological traits (i.e. population density, dispersal, reproductive characteristics, abundance, and activity pattern) (Karanth 1995; Carbone et al. 2001; Singh et al. 2020, 2021).

We studied the spatial and temporal overlap of the leopard with its potential prey species using camera traps in Kalesar National Park (KNP) situated in the foothills of Shiwalik, Himalaya. The KNP is the only protected area in Haryana state with dense forest dominated by Sal (*Shorea robusta*) and a high density of leopards (19.3 ± 5.1 individuals/100 km^2; Sehgal 2020). The KNP, a small, protected area with a high prey base, without any other sympatric large carnivore, i.e. tiger (*Panthera tigris*) and dhole (*Cuon alpines*), acts as a corridor to Simbalbara National Park and Rajaji National Park. Being the single large predator in KNP, leopards are expected to have spatio-temporal overlap with large-bodied prey species, i.e. sambar (*Rusa unicolor*) and small-bodied prey species, i.e. chital and barking deer. Our objective was (i) to study the activity pattern of leopards and (ii) to understand the spatial and temporal overlap of leopards with different-sized prey species, using photo-capture data from camera traps. The information generated from this study will help to understand the spatial and temporal activity pattern of leopards and their prey species, which is important to forest managers for the effective conservation and management of the leopard population in KNP.

Materials and methods

Study area

We conducted this study in Kalesar National Park (KNP), Haryana (Fig. 1). The area of KNP is 46.8 km^2, and it is situated in the foothills of the Shiwalik mountain range of Himalaya, North India. The park shares boundaries with two other protected areas: Simbalbara National Park (later renamed Col. Sher Jung NP) of Himachal Pradesh to the North and Rajaji Tiger Reserve of Uttarakhand East (MoEFCC: Ministry of Environment, Forest and Climate Change 2016). The park's terrain varies from plains to hills, with elevations ranging from 600 to 1100 m, and temperature varies from 5 °C in winter to 46 °C in summer (Kalsi 1998). The habitat in the park is categorized as a dry deciduous forest (Champion and Seth 1968). Sal (*Shorea robusta*) is the dominant tree species in the forest with a mixture of Rohini (*Mallotus philippensis*), sandan (*Desmodium oojjeinense*), amaltas (*Cassia fistula*), Khair (*Acacia catechu*), chhal (*Anogeissus latifolia*), and sindoor (*Bixa Orellana*). The major potential prey species found in KNP are sambar (*Rusa unicolor*), chital (*Axis axis*), barking deer (*Muntiacus muntjac*), nilgai (*Boselaphus tragocamelus*), wild boar (*Sus scrofa*), rhesus monkey (*Macaca mulatta*), and common langur (*Semnopithecus entellus*), Indian hare (*Lepus nigricollis*), peafowl (*Pavo cristatus*), and red junglefowl (*Gallus gallus*). Apart from leopard, other carnivores present are leopard cat (*Prionailurus bengalensis*), Asiatic wildcat (*Felis sylvestris*), rusty-spotted cat (*Prionailurus rubiginosus*), jungle cat (*Felis chaus*), Indian jackal (*Canis aureus indicus*), and Indian grey mongoose (*Herpestes edwardsii*), Asian palm civet (*Paradoxurus Hermaphroditus*), and small Indian civet (*Viverricula indica*). Asian elephant (*Elephas maximus*), Indian crested porcupine (*Hystrix indica*), and Indian pangolin (*Manis crassicaudata*) also occur in Kolesar.

Ethics statement

This study was conducted after getting permission from Haryana Forest Department (letter no. 2062, effective from 04–09-2017). We followed all guidelines for animal care and scientific research ethics.

Data collection

We conducted a reconnaissance survey of KNP in December 2019 by walking animal trails, roads, and seasonal water streams through documenting indirect signs (pugmarks, scats, and tree markings) of leopards. First, we marked the geo-coordinates of each sign using the Global Positioning System (GPS) Garmin etrex-20 (Garmin corp., Olathe, KS, USA). Then, we overlaid locations of indirect signs of the leopard on a 1×1 km^2 grid map in ArcMap 10.2.2 (ESRI©) to determine the spatial distribution of leopards and select camera trap locations. The inter-trap distance between the trapping stations was 0.63 km. Finally, we deployed the camera traps close to the animal trails used most frequently by carnivores to ensure a chance of detecting every leopard in the study area (Singh et al. 2021).

Camera trapping

We used 15 digital passive infrared remote camera systems (Cuddeback C1 type; WI, USA). We placed a camera trap on either side of the road to capture one flank of leopards. The sensitivity of camera traps was set minimum level, and camera traps were placed approximately 5–7 m away from the centre of the road. The camera traps had white flashes, which illuminated 30–35 m. We divided the study area into two consecutive non-overlapping blocks without any spatial gaps and sampled systematically in a phased manner. The minimum convex polygon (MCP; Fig. 1) of all the camera trapping sites covered an area of 27 km^2. We conducted the sampling from January to April 2020, with 46 days sampling period in each block. The camera traps were functional throughout the day and night during the sampling period.

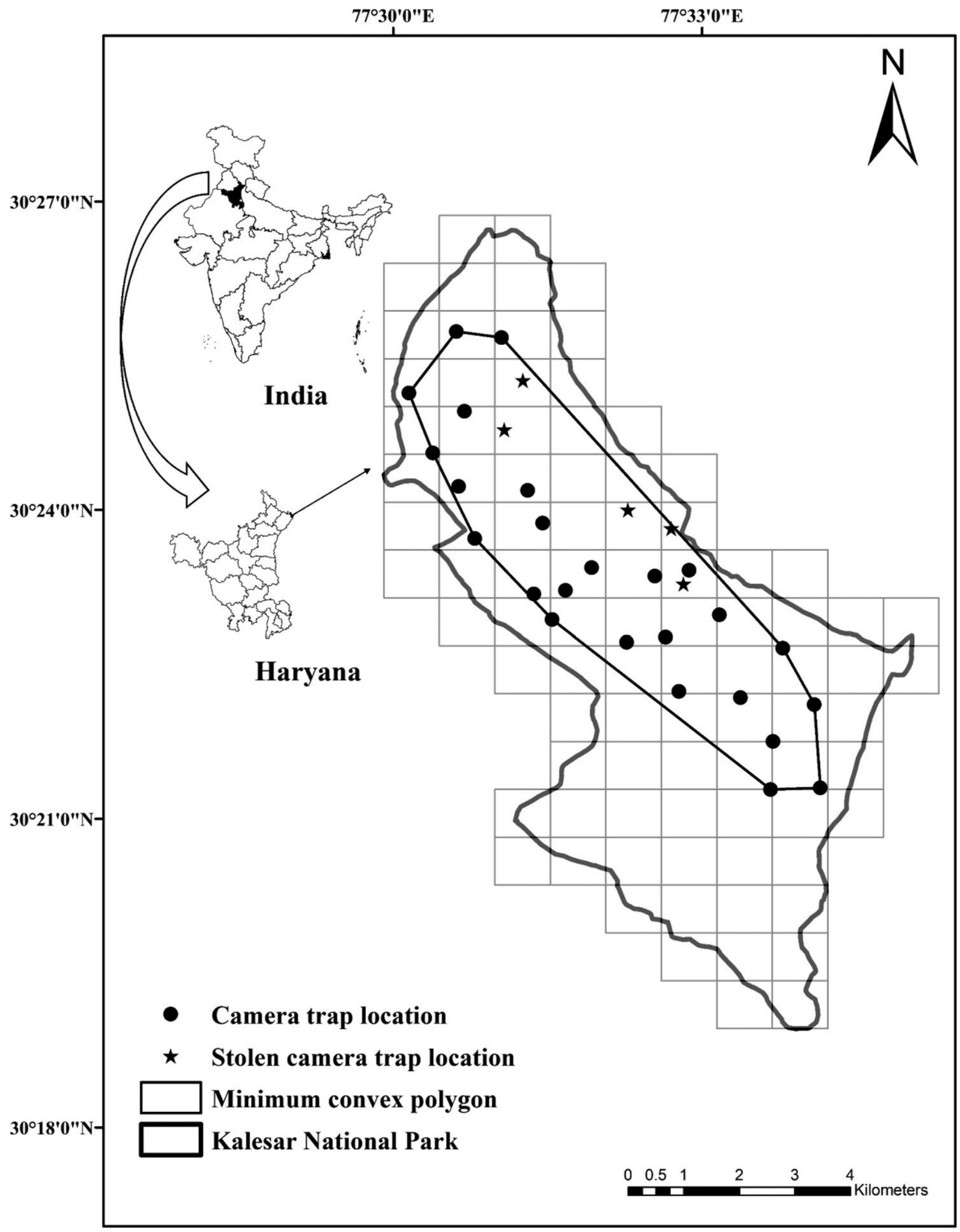

Fig. 1 Camera trap locations during the sampling period (January–April 2020) in Kalesar National Park, India

We checked camera traps twice every week to download images and replace batteries. During the sampling period, five camera traps were lost to theft (Fig. 1), and therefore, we censored the data from these locations from the analysis. We identified the species from photo-capture data and recorded the date, time, and trapping stations imprinted on each photograph. The camera trap images were independent as we considered multiple images of the same species captured at the same trapping station within ≤ 30 min of a time interval as one capture event (Linkie and Ridout 2011; Singh and Macdonald 2017). However, if two different marked individuals of the same species were captured in a photograph, we considered each individual as a different event (Mukherjee et al. 2019). We considered the independent capture events as random samples for leopard and its prey species from the underlying circular continuous temporal distributions showing the probability of a photograph being captured within any particular day interval (Ridout and Linkie 2009). We performed the Hermans-Rasson test for each species to compare if a random activity overlap was exhibited over a circadian cycle (Landler et al. 2019).

Temporal and spatial overlap

We used a non-parametric kernel density estimation method to estimate the activity pattern and overlapping coefficient (Δ) for leopard and prey species (Linkie and Ridout 2011). We estimated the analysis of activity pattern and coefficient of overlap among the daily activity pattern of leopard and its prey species using the 'overlap' package (Meredith and Ridout 2018) in R-studio (version 3.1.2; R Development Core Team 2011). The Δ is defined as the area under the curve formed by taking the minimum of the two density functions at each time point. The overlapping coefficient (Δ) ranges from 0 (no overlap) to 1 (complete overlap; Linkie and Ridout 2011). The Δ1 to Δ5 were the five different non-parametric estimators of the overlapping coefficient (Schmid and Schmidt 2006). The Δ in addition, 1 and Δ4 kernel density estimators were used for small (< 75) and large (> 75) sample sizes, respectively, whereas Δ1 and Δ2 estimators were equivalents (Linkie and Ridout 2011). We used both Δ1 and Δ4 estimators depending upon the number of independent photo-capture events. We obtained 95% confidence intervals of the overlapping coefficient by bootstrapping data 10,000 times. Information about prey species of the leopard was taken from previous literature available on food habits of leopards (Hayward et al. 2006; Harihar et al. 2011; Mondal et al. 2011; Ramesh et al. 2012; Zehra et al. 2017).

We followed the methods of Ngoprasert et al. (2012) and Allen et al. (2021) to assess the spatial overlap of leopards with their potential prey species. Relative abundance index (RAI) was calculated for leopard and its prey species and then scaled to continuous probability values ranging from 0 to 1 for each prey species at each camera trap station (Allen et al. 2021). RAI was calculated as:

$$\mathrm{RAI} = ETN \times 100$$

where E is the number of events (photo-captures) and TN is the total number of trap nights (Palmer et al. 2018). RAI gave an approximate index of abundance (Palmer et al. 2018; O'Brien et al. 2019).

We performed logistic regression analyses by taking leopard presence as the dependent variable and prey probability as an independent variable. We used the area under the curve (AUC) of receiver operating characteristic plots (Fielding and Bell 1997) to compare the spatial overlap of prey species, which is a measure of overall fit and ranges from 0.5 (random) to 1.0 (perfect fit). We plotted the spatial and temporal overlap of the leopard with its potential prey species to determine which prey species were preferred (Allen et al. 2021). The prey species falling in the upper right quadrant of the plot (high spatial and temporal overlap) suggested the most encountered and potentially the most preferred prey species. The species placed in the upper left (high temporal and low spatial overlap) and lower right (low temporal and high spatial overlap) quadrants indicated potential alternative prey species encountered less in space and time. The lower left quadrant (low spatial and temporal overlap) suggested species that were rarely encountered and not preferable prey species.

We estimated the spatial and temporal composite scores by calculating the mean of the spatial and temporal overlap values (Allen et al. 2021). A higher value of composite score indicated a higher encounter rate of leopard with a prey species and potentially higher prey preference, which was used to rank the potential prey species. For calculating the spatial adjusted composite score, we provided additional weight to the spatial overlap value, as the spatial overlap is a fundamental aspect of niche selection and resource partitioning between the leopard and its potential prey species (du Preez et al. 2017; Allen et al. 2021). The spatial adjusted composite score was calculated as:

$$\text{Spatial adjusted composite score} = (\text{spatial overlap} \times 0.6) + (\text{temporal overlap} \times 0.4)$$

Finally, we calculated the spatial and mass adjusted composite scores, including prey mass. For calculating mass adjustment value, we multiplied the spatial adjusted composite score with 1.1 for prey species within the preferred prey mass range of leopard (10–40 kg; Hayward et al. 2006) and (spatial adjusted composite score × 0.9) for potential prey outside the given range. Prey mass values were obtained from Mondal et al. (2011) and Kshettry et al. (2018). Spatial and mass adjusted composite score was calculated as:

$$\text{Spatial and mass adjusted composite score} = ((\text{spatial overlap} \times 0.6) + (\text{temporal overlap} \times 0.4)) \times \text{mass adjustment}$$

We then ranked the potential prey species based on the estimated composite score. The higher value of composite scores indicated a higher encounter rate and potentially higher prey preference (Allen et al. 2021).

Results

Sampling effort

We had a total sampling effort of 1150 camera trap nights at 25 camera trap stations, documenting 1481 photo-captures of leopards and potential prey species. The 199 (90 left flank and 109 right flanks) leopard photo-captures constituted 13.4% of total photo-captures. The major prey species in photo-captures were sambar (29.9%), chital (19.9%), wild boar (14.4%), rhesus macaque (12.7%), peafowl (8.4%), and barking deer (1.3%). According to the Hermans-Rasson test, all species had significantly different activity overlaps from random (Table 1).

Table 1 Summary of Hermans-Rasson uniformity test to compare if a random activity overlap was exhibited over a circadian cycle for leopard and its prey species from camera trap data in Kalesar National Park, India

Scientific name	Common name	Hermans-Rasson test		
		N	*T*	$P < 0.01$
Axis axis	Chital	293	345.8	0.0001
Macaca mulatta	Rhesus macaque	187	224.8	0.0001
Muntiacus muntjak	Barking deer	20	27.8	0.00010
Panthera pardus	Leopard	199	218.1	0.0001
Pavo cristatus	Peafowl	124	134.1	0.0001
Rusa unicolor	Sambar	441	470.6	0.0001
Sus scrofa	Wild boar	212	243.7	0.0001

N is the number of independent events (≤30-min interval between events)

Activity patterns

Leopards showed bimodal activity peaks at 9:00 h and 17:00 h and less activity during the middle of the day (Fig. 2). The highest degree of activity overlap was observed between leopard and chital [Δ4 = 0.87 (0.80–0.92)] (Fig. 2a) followed by wild boar [Δ4 = 0.82 (0.74–0.87)] and sambar [Δ4 = 0.81 (0.72–0.84)] (Fig. 2b, c). Barking deer also showed a high degree of overlap [Δ1 = 0.79 (0.69–0.96)] with leopard (Fig. 2d; Table 2). The other species had notably lower levels of activity overlap with leopard, Δ4 = < 0.63.

Relative abundance index and composite

Wild boar (0.76) and sambar (0.75) had the highest spatial overlap with leopard, followed by peafowl (0.68; Table 2).

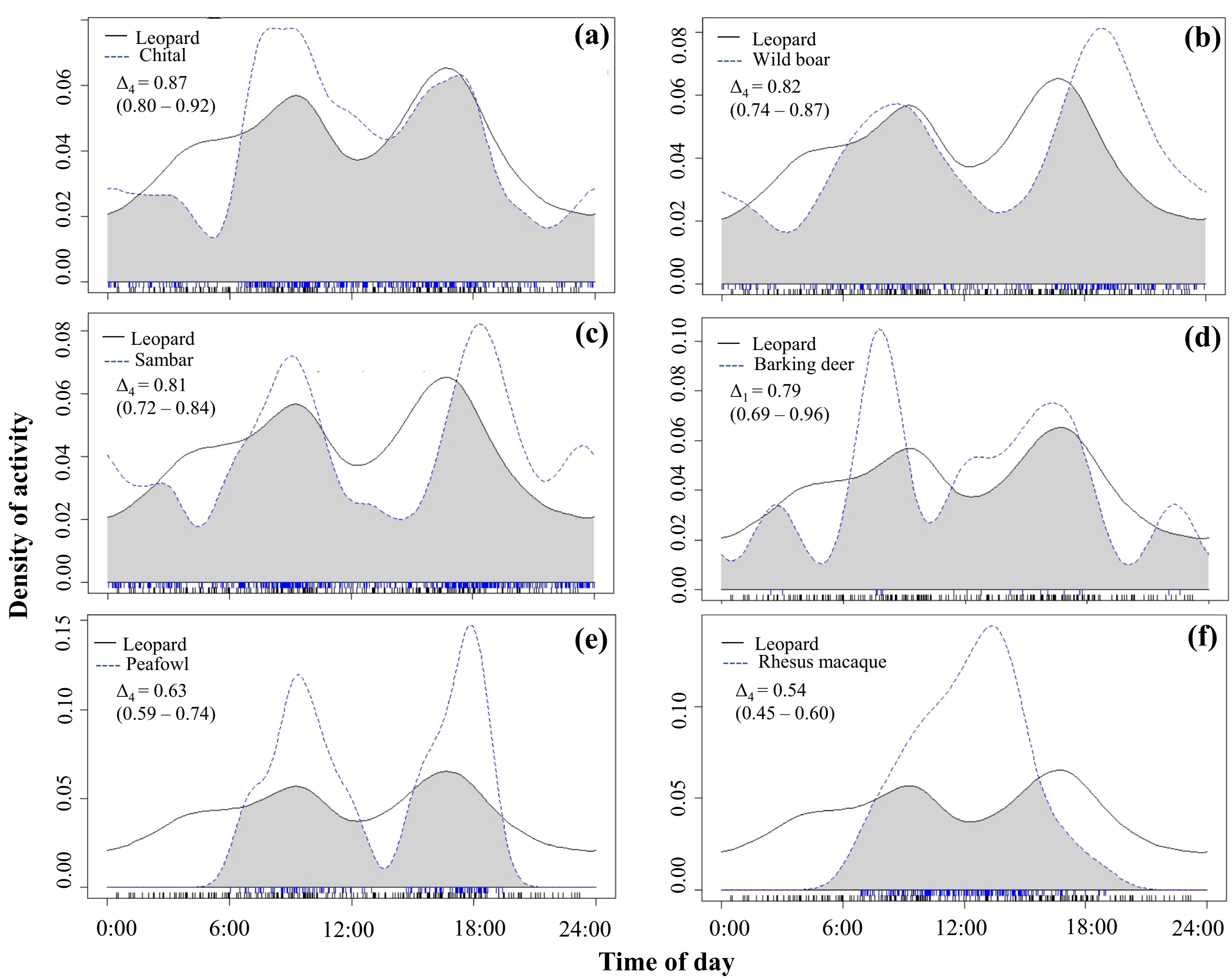

Fig. 2 Temporal overlap between the leopard and its prey species (**a**. chital, **b**. wild boar, **c**. sambar, **d**. barking deer, **e**. peafowl, **f**. rhesus macaque) using kernel density estimates in Kalesar National Park, India. The solid lines represent the kernel density estimates for leopard and the dashed lines represent the kernel density estimates for indicated prey species. The overlap coefficient is the area under the minimum of the two density estimates, as indicated by the shaded area in each plot

Table 2 The index showing potential prey species of leopard in Kalesar National Park, India, including relative abundance (detection events/100 trap nights), temporal overlap (CI), spatial overlap, spatial adjusted composite score, and spatial and prey mass adjusted composite score. The higher value of composite scores indicates a higher encounter rate and potentially higher prey preference

Species	Relative abundance	Temporal overlap (*CI)	Spatial overlap	Spatial and temporal composite score	Spatial adjusted composite score	Spatial and prey mass adjusted composite score
Wild boar	18.43	0.82 (0.74–0.87)	0.76	0.79	0.78	0.86
Sambar	38.34	0.81 (0.72–0.84)	0.68	0.74	0.73	0.66
Peafowl	10.78	0.63 (0.9–0.74)	0.75	0.69	0.7	0.63
Chital	25.47	0.87 (0.80–0.92)	0.19	0.53	0.46	0.51
Barking deer	2.17	0.79 (0.69–0.96)	0.06	0.42	0.35	0.38
Rhesus macaque	16.26	0.54 (0.45–0.60)	0.12	0.33	0.29	0.26

*CI, confidence interval

We plotted the values of spatial and temporal overlap of the leopard with its potential prey species (Fig. 3). Wild boar, peafowl, and sambar were present in the upper right quadrant (high spatial and temporal overlap), indicating potentially preferred prey. In contrast, chital, rhesus macaque, and barking deer fell in the upper left quadrant (high temporal but low spatial overlap), suggesting potential alternative prey species (Fig. 3). Based on the composite scores, wild boar was ranked with the highest spatial adjusted composite score and the highest spatial and prey mass adjusted score, followed by sambar and peafowl (Table 2).

Discussion

This study predicts potential prey preferences of leopards using motion-sensitive camera traps. Studies in India suggested that the leopard was active throughout the day in Mudumalai Tiger Reserve (Ramesh et al. 2012),

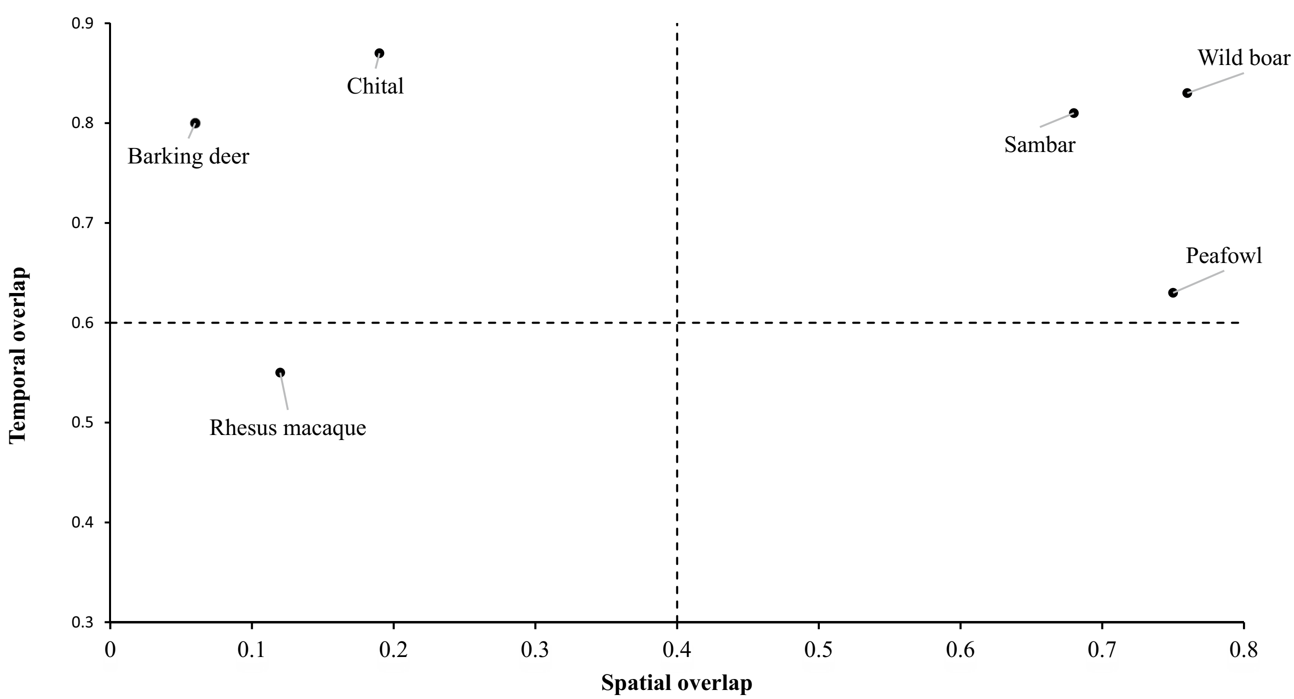

Fig. 3 The spatial and temporal overlap of leopard with its potential prey species (the sambar, wild boar, and peafowl showing high spatial and temporal overlap suggested the most encountered and potentially the most preferred prey species. The barking deer and chital showing high temporal and low spatial overlap indicated potential alternative prey species encountered less in space and time. The rhesus macaque showing low spatial and temporal overlap suggested species that were rarely encountered and not preferable prey species) in Kalesar National Park, India

crepuscular and nocturnal activity in Gir National Park and Wildlife Sanctuary (Chaudhary et al. 2020). Leopards in KNP were active throughout the day and night but showed more activity during the daytime, which may be due to more prey activity during the daytime hours. The temporal overlap of leopard in KNP was highest with chital followed by wild boar, sambar, and barking deer, whereas spatial overlap of the leopard was highest with wild boar followed by peafowl, sambar, and chital. The leopard showed a positive correlation of activity with sambar and gaur but not with chital and langur and exhibited a positive spatial correlation with its prey species (i.e. chital, gaur, langur, and sambar) in Mudumalai Tiger Reserve (Ramesh et al. 2012). In Gir, the leopard had the highest temporal overlap with the sambar, followed by the wild boar and chital, while the spatial overlap of the leopard was highest with the sambar followed by the chital, nilgai, and wild boar (Chaudhary et al. 2020).

In early ecological studies, the temporal overlap was considered a valid method to determine prey preferences, but O'Brien et al. (2003) and Linkie and Ridout (2011) observed that the temporal overlap was more effective when combined with spatial overlap. The higher spatio-temporal overlap between predator and prey species does not necessarily suggest prey preference but rather high encounter rates, an important factor in predicting prey preferences (Fortin et al. 2015; Allen et al. 2021). Leopards are energy maximizers in prey-rich areas (Karanth and Sunquist 1995; Hayward et al. 2006) and select prey, age, and sex classes that are highly abundant and easiest to hunt (Bothma and Coertze 2004). Due to this reason, leopards often prefer medium-sized ungulates such as chital as their prey, but this will vary across study areas (Hayward et al. 2006).

We calculated that each composite score suggested a similar ranking for potential prey species, with wild boar and sambar being ranked highest, followed by peafowl, chital, and barking deer. Previous studies on leopard food habits in India suggested that chital and sambar were the most frequent prey in the leopard diet, followed by wild boar, langur, and peafowl (Zehra et al. 2017). The greater spatial overlap and composite scores for peafowl may be due to its widespread distribution across camera trap sites, which inflated its spatial overlap with leopard and overestimated prey preference. Conversely, the spatial overlap of chital was less due to its confined distribution to a specific habitat (grasslands), which underestimated its preference as prey in KNP despite their high abundance. Low overlap and composite scores for barking deer and rhesus macaque indicated them as an alternative prey species. However, camera trap images revealed leopard carrying rhesus macaque kill, which indicated that leopards prey on rhesus macaque in KNP (Fig. 4).

A study on leopard diet selection from the human-use landscape in North-Eastern India indicated that rhesus macaque contributed the highest relative biomass (10%) among wild prey (Kshettry et al. 2018). It has been a long-standing myth that primates are not important prey to leopards (Hunter 2015), yet there is growing evidence from other places that primates are frequently predated upon example (Havmøller et al. 2020a, b). Havmøller et al. (2020a) also found the least temporal overlap between leopards and primates as this is not intuitive at all but could indicate predator avoidance by primates.

Our study showed that leopards exhibit bimodal peaks and high temporal overlap with chital followed by wild boar and sambar, while high spatial overlap with wild boar and sambar. We used the spatio-temporal overlap of leopard and

Fig. 4 Photo-capture of leopard predate on primates (rhesus macaque) is clear evidence of how leopards predate on primates, and low temporal overlap could indicate avoidance in Kalesar National Park, India

its prey species with composite scores to study interspecific competition and prey preferences of leopard from camera trap data. However, we placed our camera traps at roads and trails, limiting the scope of studying predator–prey interactions (Havmøller et al. 2020a, b). Prey species of large carnivores are often more threatened in developing countries due to hunting, habitat loss, and high densities of the human population (Wolf and Ripple 2016). Recent studies showed a continuous decline in leopard populations due to prey loss, which ultimately altered their food habits and led to their being vulnerable globally (Wolf and Ripple 2016; Sandom et al. 2018; Creel et al. 2018). The conservation of large carnivores could be achieved by enforcing scientific management and effective conservation of protected areas. Based on the above findings, we suggest the forest department focuses more on wild boar, sambar, and chital, to ensure that an adequate prey base is available for sustaining the leopard population in the park.

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Author contribution RSK developed the study design and secured the funding. JJS, DK, RSK, and RS contributed to the data collection. JJS, RSK, RS, and MLA participated in the data analysis. All authors participated in the draft and approved the final manuscript.

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Declarations

Ethical approval This manuscript has been approved by all co-authors.

Conflict of interest The authors declare no competing interests.

Research involving human participants and animals The research complies with the guidelines or rules for animal care and use for scientific research.

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