Original Study

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Diet and activity pattern of leopard in relation to prey in tropical forest ecosystem

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Abstract: Understanding the predator–prey relationship is essential for implementing effective conservation management practices on threatened species. Leopard is a threatened apex mammalian predator that plays a crucial role in ecosystem functions in India's tropical forest. We assessed the diet and activity pattern of leopards in relation to their prey using diet analysis and camera trapping data from Similipal Tiger Reserve, eastern India. Our results indicated that leopard prefers medium-sized prey such as wild pig, common langur and barking deer represented 60% of the total biomass consumed collectively. Results of 6413 camera trap night in 187 locations revealed that leopards showed cathemeral activity pattern and exhibited positive co-occurrence pattern and significant spatial and temporal overlap with their main prey, the wild pig. However, leopards showed very low spatial and temporal overlap with the second main prey, the common langur. Leopards avoided humans and showed low spatial and temporal overlap with humans. Our findings reveal that a trade-off might drive leopard activity between consuming prey and avoiding anthropogenic disturbances like human activity.

Keywords: camera trap; diet; leopard; *Panthera pardus*; predator-prey; spatio-temporal overlap.

1 Introduction

Apex predators play a critical role in any given ecosystem due to their trophic cascade effects on prey species (Ripple et al. 2014). Moreover, large carnivores can potentially influence prey abundance, distribution and behaviour through predation (Ripple et al. 2013). Predation risk may impose substantial costs on prey species' behavioural response, including spending more on antipredator behaviour, limiting the time available for foraging and changing time allocation patterns (Ordiz et al. 2013). Despite several limitations such as imperfect detections (Rowcliffe and Carbone 2008; Stephens et al. 2015) and independence of sampling sites (Wearn et al. 2013), camera-trapping surveys have been widely used to investigating predator–prey interaction using photographic capture data (Delibes-Mateos et al. 2014; Linkie and Ridout 2011; Marinho et al. 2018; Porfirio et al. 2016; Ramesh et al. 2012a; Ross et al. 2013; Yang et al. 2018). Studies evaluating interactions between large predators and their prey through camera-trapping have found significant spatial and temporal overlaps (Dou et al. 2019; Linki and Ridout 2011; O'Brien et al. 2003; Ramesh et al. 2012a; Ross et al. 2013). These investigations have suggested that predators can adjust their activity to increase the probability of encounters with their prey, minimizing the energetic costs of foraging (Eriksen et al. 2011; Foster et al. 2013; Harmsen et al. 2011; Porfirio et al. 2016). Likewise, prey may alter their activity patterns in response to predators (Carter et al. 2015; Ngoprasert et al. 2007).

The leopard (*Panthera pardus*), categorized globally as Vulnerable on the IUCN Red List, has the widest distribution of any wild felid species, ranging from western and southern Africa to the Russia Far East and Java (Stein et al. 2016). It is primarily a result of the species' high adaptability, as it can occupy diverse ecosystems ranging from tropical rainforests to boreal forests and arid savannahs (Stein et al. 2016). In the tropical forest of India, the leopard is one of the apex mammalian predators. Previous studies on the leopards' prey preferences in different areas revealed a wide-ranging diet from arthropods to large mammals, and medium-sized ungulates generally

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dominate their diet (Hayward et al. 2006; Johnsingh 1992). However, the activity pattern of these prey species and their spatio-temporal interaction with leopard remain unclear.

In the Indian subcontinent, most of the studies of spatial and temporal activity pattern have focused on the interactions within large carnivore guild (lion, tiger, leopard and wild dog) with their potential prey (Chaudhary et al. 2020; Kafley et al. 2019; Karanth et al. 2017; Ramesh et al. 2012a); where subordinate competitors like leopard reduce the limiting effects of dominants competitors by avoiding them in spatial and temporal scale. However, information is still scarce concerning leopard activity pattern and their prey in the absence of any other large carnivores. To help this information gap, we investigated the diet and activity of the leopard population in relation to their spatio-temporal activity of prey in Similipal Tiger Reserve, eastern India. Palei et al. (2016a) found a very low population abundance of tigers in the Similipal Tiger Reserve, which indicates the limited role on leopard activity and space use. In the absence of any large carnivore, subordinate carnivore may maximize hunting opportunities rather than as a tactic to avoid interspecific conflicts (Ross et al. 2013). This condition provides a unique opportunity to assess the predator–prey relationship of leopard and their prey, which is essential to understand their ecology and conservation.

We used scat analysis and camera trapping to study the diet and spatio-temporal interaction of leopard and prey. We predicted that: (i) medium-sized prey species would dominate the leopard diet; and (ii) high spatial and temporal overlap between the leopard and their dominant prey species.

2 Materials and methods

2.1 Study area

The study was carried out between November 2012 and October 2013 in the Similipal Tiger Reserve (20° 17′–22° 34′ N and 85° 40′–87° 10′ E), located in the state of Odisha in eastern India (Figure 1). The tiger reserve is divided into two distinct zones: a core reserve area of 1194.75 km^2 and a surrounding buffer zone of 1555.25 km^2 (Dash and Behera 2018). Similipal Tiger Reserve has been included as a part of the World Network Biosphere Reserve (WNBR) by UNESCO, well known for its biodiversity with species diversity of 70 species of mammals, 365 species of birds, 61 species of reptiles, 21 species of amphibian, 66 species of fishes and 106 species of butterflies (Baliarsingh et al. 2013; Mishra et al. 2016; Nair 2007; Palei et al. 2016a). The tiger reserve is dominated by sal (*Shorea robusta*) plants with semi-evergreen, moist and dry deciduous forests occurring successively along a rainfall gradient (Saxena and Brahmam 1989). The climatic condition of the study area experiences three distinct seasons: monsoon (July–September), winter (October–February) and summer (March–June). The area receives an average annual rainfall of 1850 mm and the temperature ranged from 3 °C in winter to 38 °C in summer.

Similipal Tiger Reserve is one of the high-priority areas for tiger conservation (Level I, Tiger Conservation Units) and has a known leopard population (Wikramanayake et al. 1998). The wild ungulate species in the study area are gaur, sambar, spotted deer (*Axis axis*), wild pig, barking deer (*Muntiacus muntjak*) and mouse deer (*Moschiola indica*) and two primate species: common langur (*Semnopithecus entellus*) and rhesus macaque (*Macaca mulatta*) which serve as prey for the carnivores according to Palei et al. (2016b).

2.2 Methods

2.2.1 Scat collection and analysis: The diet of leopard was determined by analysis of scats that were opportunistically collected by walking along roads and trails. Based on size (diameter and length) and other secondary characteristics such as pug marks and scrapes, leopard scats were differentiated from other carnivore species (Rabinowitz 1989; Ramesh et al. 2012b). Leopard scats were coiled more than tiger scats, with relatively shorter distances between successive constrictions within a single piece of scat (Harihar et al. 2011; Johnsingh 1992; Karanth and Sunquist 1995; Ramesh et al. 2012b). A total of 123 scat samples were collected and analysed. After drying, scat samples were preserved in the tagged polythene bag and later washed thoroughly using 1 mm sieve. The undigested prey remains such as hairs, teeth, bones, hooves, quills, claws, etc. were separated (Edgaonkar and Chellam 2002; Mondal et al. 2011). Prey hair remains undamaged in carnivore scats can be used to identify the prey species consumed (Harihar et al. 2011; Ramesh et al. 2012b). At least 20 individual hairs were picked at random from each scat and identified by microscopic examination of the cuticular pattern and the medulla using reference publications (Bahuguna et al. 2010; Chakraborty et al. 1999; De et al. 1998; Kuhn and Meyer 2010).

To quantify the scat content, we calculated the frequency of occurrence (F) of the various prey species (the percentage of the total number of scats in which a prey item was detected). However, this method is known to be misleading (Harihar et al. 2011). We calculated biomass (D) and the number of prey individuals (E) consumed by leopards, using Ackerman's equation, $Y = 1.98 + 0.035X$, where Y = mass of prey (kg) per leopard scat sample and X = average mass of an individual of a particular prey species (Ackerman et al. 1984). We obtained the average weight (X) of prey species from Harihar et al. (2011) and Karanth and Sunquist (1995).

A species accumulation curve based on scat samples was plotted to assess whether the number of scats analysed accurately reflected the leopard's diet. We used the *specpool* and the *specaccum* functions in the R package *vegan* to get extrapolated species richness estimates and species rarefaction curves based on occurrence data by randomizing 1000 times all scat samples. We used the Ivlev index (E; Ivlev 1961) to determine the prey preference of leopards: $E = (r_i - p_i)/(r_i - p_i)$, where r_i is the proportion of the i-th prey item consumed and p_i is the proportion of the i-th prey type available in that environment. The index values range from −1 to +1, with positive values indicating preferences and negative values indicate avoidance. We obtained information on prey densities (availability) estimated by the National Tiger Conservation Authority (NTCA) and

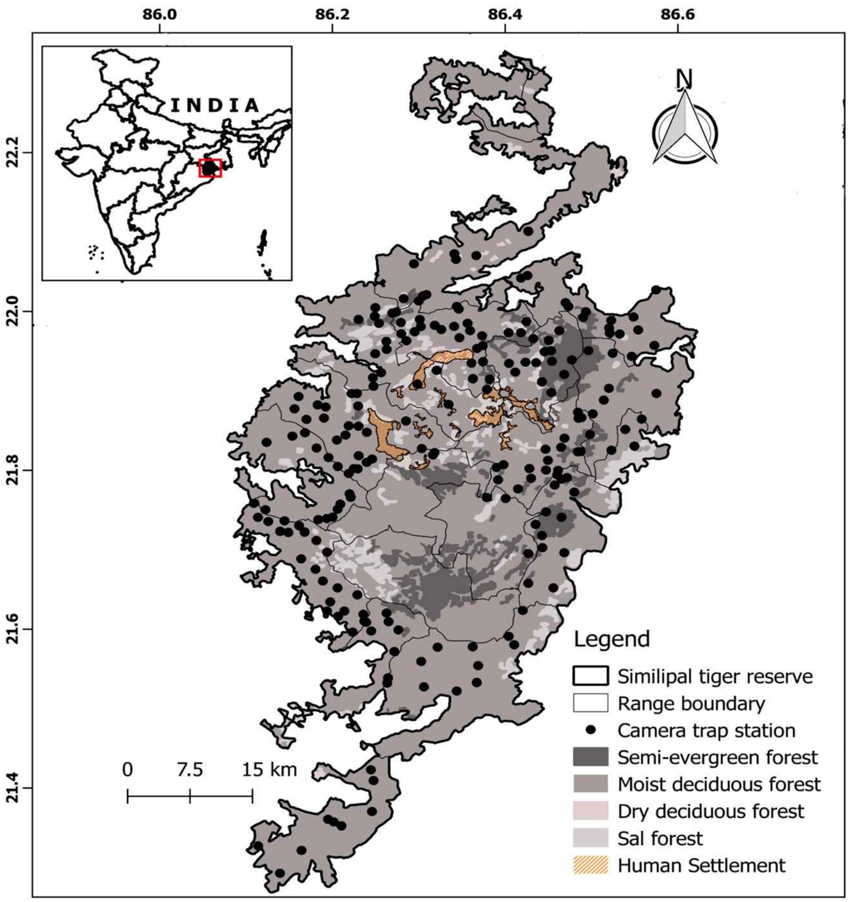

Figure 1: Study area showing locations of camera trap stations in the Similipal Tiger Reserve, India.

Wildlife Institute of India (WII) as part of the All India Tiger Monitoring Programme, using line transect surveys and distance sampling methods (Jhala et al. 2015).

2.2.2 Camera trap data collection: To ascertain the status of large carnivores and their prey, we established camera trap stations covering the 16 forest ranges in the study area (Figure 1). We placed one camera trap in each camera trap station (Moultry D55, GameSpy Digital Camera, Alabaster, USA) along roads, animal trails, and footpaths. Cameras were set to operate 24 h per day with programmed to delay sequential photographs by 30 s recording time, date and temperature for each exposure. We checked all camera trap stations at 10–14 days intervals for battery replacement and photo download. To avoid pseudoreplication, animal detections were considered independent if it occurred more than 30 min after the last series of photographs for a species, unless individuals were distinguishable by unique pelage patterns or colours and different sex or age class (O’Brien et al. 2003; Rich et al. 2017; Yang et al. 2018). Photos with more than one individual of similar species were treated as a single event for the species.

Spatio-temporal activity patterns of leopard and seven prey species were extracted from the camera data, including five ungulates (sambar, spotted deer, barking deer, mouse deer and wild pig), one primate (common langur) and one rodent (porcupine). Several previous studies demonstrated the importance of these potential prey species in leopards’ diet in India’s tropical forest (Hayward et al. 2006; Johnsingh 1992; Ramesh et al. 2012b).

2.2.3 Leopard and prey species co-occurrence pattern: The leopard and prey species co-occurrence patterns were analysed using the probabilistic model of species co-occurrence (Veech 2013), which allows analytical (without randomization or simulation) determination of the probability that two selected species co-occur at a frequency either less than or greater than the observed frequency of co-occurrence. These probabilities can be obtained analytically under the condition where a species probability of occurrence at each site is equal to its observed frequency among all sites. When the observed frequency of co-occurrence is significantly large and greater than expected, a positive association is indicated; if co-occurrence is significantly small and less than expected, a negative association is indicated; or if observed and expected co-occurrence is not significantly different and approximately equal to expected a random association is indicated (Veech 2013). We analysed to determine the pairwise association between leopard and prey species. Analysis of species co-occurrence patterns was conducted using the R packages *co-occur 1.3* (Griffith et al. 2016).

2.2.4 Leopard and prey species spatial overlap: To investigate the spatial overlap between leopard and prey species, we calculated the relative abundance index (*RAI*) for each camera trap site as the number of detections per 100 camera-trap days for every species (O’Brien et al. 2003; Pianka 1973). The data were organized into a matrix where each row represents a species, each column represents a camera trap site, and each entry represents a *RAI* of the species. In this matrix, we calculated the average pairwise overlap among leopard and its prey species using the Pianka niche overlap index (Pianka 1973):

$$O_{jk} = O_{kj} = \sum P_{ij} P_{ik} \Big/ \left(\sum P_{ij}^2 \sum P_{ik}^2\right)^{1/2}$$

where O_{jk} is the Pianka niche overlap index of species j over species k, O_{jk} is the reciprocal overlap of k over j. P_{ij} is the proportion of the ith resource used by j, and P_{ik} is the proportion of the ith resource used by k. Pianka's index (O) varies between 0 (total separation) and 1 (total overlap).

We used the R package *ecosimR* (Gotelli and Ellison 2013) to calculate the Pianka niche overlap index to test the leopard and prey species' spatial overlap. We tested for significance spatial niche overlap by comparing observed values with values obtained by randomizing the original matrices (1000 interactions), using the default procedure (RA3) of the ecosimR (Gotelli and Ellison 2013). For each pair of species compared, if the observed O value greater than expected value, we concluded the two populations were aggregated distribution and spatial overlap. If the observed O value was less than expected value, we concluded that the populations were segregated distribution and spatial overlap (Surkova et al. 2018). For each species pair, we also calculated the standardized effect size (SES), as follows:

$$\text{SES} = \text{observed index} - \text{mean of simulated index}/$$
$$\text{standard deviation of simulated index}$$

Following this, 1000 randomized species pairs values were averaged, where the positive SES values indicate aggregation and negative SES values indicate segregation.

2.2.5 Leopard and prey species daily activity pattern and overlap: We followed two steps to study the daily activity pattern and temporal overlap between the leopard and prey species (Linkie and Ridout 2011; Ridout and Linkie 2009). First, a non-parametric kernel-density estimation was used to describe temporal activity of the leopard and their prey species. This method considers each photographic record as a random sample of an underlying continuous distribution, instead of grouping photographic records in blocks of predefined discrete-time categories (Ridout and Linkie 2009). Second, the coefficient of overlap, Δ, which ranges from 0 (no overlap) to 1 (complete overlap) were used to measure the overlap for leopard and its prey species (Ridout and Linkie 2009). We used $\hat{\Delta}_1$ for small samples (<50 detections); otherwise, we used $\hat{\Delta}_4$ as suggested by Linkie and Ridout (2011) and Ridout and Linkie (2009). The overlap accuracy coefficient was estimated creating 95% confidence intervals generating 1000 simulations with the nonparametric estimator bootstraps (Ridout and Linkie 2009). The analysis was performed using package *overlap* implemented in R version 3.5.1 (Meredith and Ridout 2017).

3 Results

3.1 Diet composition

In total, 123 leopard scats were collected from the study area. A total of 145 individual prey items were identified, representing 11 mammalian prey species. Most (82.1%) scats from leopards contained only one prey item, whereas the remainder 17.9% of scats contained two prey items. The species rarefaction curves reached the asymptote and stabilized, indicating that sample size is sufficient to support the conclusion (Figure 2). The wild pig was the most dominant and common langur was the second most prey item in the frequency of occurrence and biomass consumed in scats (Table 1). Leopard consumed more individual common langurs than all other prey species (Table 1). Prey preference analysis was restricted to three species (Common langur, barking deer and sambar) for which abundance data were available. Ivlev index values indicated that leopards showed a weak positive preference for common langurs (+0.20), neutral for barking deer (+0.07) and avoidance for sambars (−0.40).

3.2 Species co-occurrence pattern

Twenty-four of the 211 camera trap stations that we used for analyses were excluded due to stolen (11), damage by poachers or elephants (8), and malfunctioned (5). The total survey effort comprised 6413 trap nights from the remaining 187 camera trap stations with an average period of 34.48 ± 10.55 days (mean ± SD). We classified a total of 3763 independent photographs and omitted 13 unclear or distorted photos from the analysis. We obtained 108 independent detections of leopard, 417 of barking deer, 290 of wild pig, 231 of common langur, 89 of sambar, 86 of the

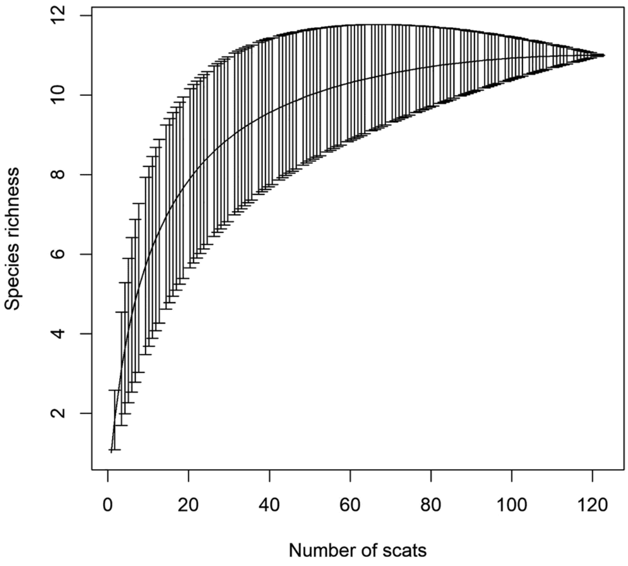

Figure 2: Sample based rarefaction curve for prey species richness found in the scats of the leopard (mean and standard deviations) in Similipal Tiger Reserve. Values represented in the curves are means with standard deviations (*SD*) as vertical bars. Mean and standard deviation is computed based on 1000 randomized samples.

Table 1: Prey species composition of leopard diets ($n = 123$) and their frequency of occurrence (F), average body weight (X), correction factor of weight per collected scat (Y), biomass consumed (D) and number of prey individual consumed (E).

Prey species	Body weight (kg) (X)	Frequency of occurrence (%F)	No. of collectable scats per kill (Y)	Biomass consumed ($D = F \times Y$ as %)	Prey individual consumed ($E = D/X$ as %)
Wild pig	40	33.3	3.4	30.7	9.9
Common langur	10	29.3	2.3	18.7	24.1
Barking deer	20	14.6	2.7	10.7	6.9
Sambar	150	8.9	7.2	4.6	1.5
Mouse deer	3	8.1	2.1	2.3	20
Spotted deer	50	7.3	3.7	7.5	1.9
Porcupine	12	6.5	2.4	4.3	4.6
Indian hare	2	4.1	2.1	2.3	14.7
Rhesus macaque	7	2.4	2.2	1.5	2.7
Indian grey mongoose	1.5	1.6	2	0.9	7.8
Indian giant squirrel	2	1.6	2.1	0.9	5.9

porcupine, 51 of mouse deer, 30 of spotted deer, and 955 of human.

The leopard was detected at 56 (percent of occurrence = 29.95) out of 187 camera trap stations from the camera trap data. For the focal prey species, percent of occurrences were recorded for barking deer (54%), wild pig (51.3%), langur (39%), porcupine (24.1%), Sambar (16%), mouse deer (11.8%) and spotted deer (6.4%). We detected the leopard with all prey species combined in 27.8% (52/187) of the camera trap stations. For individual prey species, it co-occurred most with the wild pig (21.4%), then barking deer (19.8%), common langur (13.9%), porcupine (11.2%), sambar (7%), mouse deer (4.8%) and spotted deer (3.2%).

We investigated seven pairwise relationships among leopards and their prey in probabilistic co-occurrence analysis. Except the predator–prey pairs included leopard-wild pig ($P_{gt} = 0.000$), leopard-barking deer ($P_{gt} = 0.022$) and leopard-porcupine ($P_{gt} = 0.005$), which exhibit positive co-occurrence patterns, the remaining pairs have a random species co-occurrence pattern (Table 2).

3.3 Spatial overlap

The pairwise spatial overlap values were low (0.09–0.40) (Table 3). Most of the observed overlap values were significantly higher than those expected overlap by chance with the Randomization Algorithm (RA3) showing evidence of spatial overlap. Moreover, the spatial overlap seemed to be non-random only for the leopard-wild pig ($P = 0.026$) and leopard-porcupine ($P = 0.001$) (Table 2). Leopards spatially overlapped with wild pig ($O = 0.40$) to a greater extent than with porcupine ($O = 0.20$) (Table 3, Figure 3).

Table 2: Results of the co-occurrence probability model of leopard, prey species and human in Similipal Tiger Reserve, Odisha, India.

Species	Obs_cooccur	Prob_cooccur	Exp_cooccur	P *lt*	P *gt*
Leopard and Hanuman langur	26	0.117	21.9	0.934	0.117
Leopard and Wild pig	40	0.154	28.7	0.999	0.000
Leopard and Sambar	13	0.048	9.0	0.972	0.065
Leopard and Barking deer	37	0.162	30.2	0.990	0.022
Leopard and Spotted deer	6	0.019	3.6	0.966	0.109
Leopard and Mouse deer	9	0.035	6.6	0.922	0.170
Leopard and Porcupine	21	0.072	13.5	0.998	0.005
Leopard and Human	46	0.219	41.0	0.978	0.05

Obs-cooccur, Prob_cooccur, and Exp_cooccur represent the number of sites where leopard and prey species co-occur, the probability of co-occurrence of the leopard and prey species, and the number of expected sites where both co-occur, respectively; P *lt* and P *gt* indicate whether there was a significant negative or positive co-occurrence between leopard and prey species, respectively.

Table 3: Spatial overlap analysis (Pianka's index) based on 1000 randomizations for leopard, prey species and human in Similipal Tiger Reserve, Odisha, India.

Species	Spatial overlap test values					
	Observed overlap	Expected overlap ± variance	O < E	O > E	P (O < E)	SES
Leopard and Hanuman langur	0.175	0.178 ± 0.003	536	464	0.464	−0.047
Leopard and Wild pig	0.402	0.291 ± 0.002	974	26	**0.026**	2.059
Leopard and Sambar	0.099	0.107 ± 0.004	556	444	0.444	−0.119
Leopard and Barking deer	0.255	0.199 ± 0.003	840	160	0.160	0.965
Leopard and Spotted deer	0.174	0.094 ± 0.003	887	113	0.113	1.313
Leopard and Mouse deer	0.203	0.134 ± 0.003	864	136	0.136	1.136
Leopard and Porcupine	0.208	0.137 ± 0.000	999	1	**0.001**	6.325
Leopard and Human	0.286	0.276 ± 0.002	590	410	0.41	0.194

O < E (observed < expected), species pair in which the observed index of overlap was less than expected by chance; O > E, species pair in which the overlap index was greater than expected by chance. Values of *P* in bold signify that there is significant difference between the species pair. SES, standardized effect size.

3.4 Temporal activity and overlap

Temporal activity pattern based on camera trap data showed that leopards were active at all periods, with most detections occurring at night (38%, Figures 4 and 5). Activity density functions revealed two activity peaks; the first peak was observed from late afternoon to midnight and another peak in the early morning during sunrise (Figure 5). They exhibited reduced activity during the hottest hour of the day at midday. For the prey species, strongly diurnal patterns were observed in common langur (94.4%) and followed by barking deer (58%) while mouse deer and porcupine exhibited strongly nocturnal patterns with 88.2 and 84.9% of detections, respectively and followed by sambar (73%) and wild pig (53.1%). Spotted deer were active at all periods, with maximum detections (40%) occurring during the night (Figures 4 and 5). The coefficient of activity overlap of leopard and their prey revealed that leopard had a high overlap with wild pig ($\hat{\Delta}_4 = 0.79$) but low overlap with common langur ($\hat{\Delta}_4 = 0.43$) (Figure 5). Graphical representation of the overlap of other prey species and humans can be found in Figure 5.

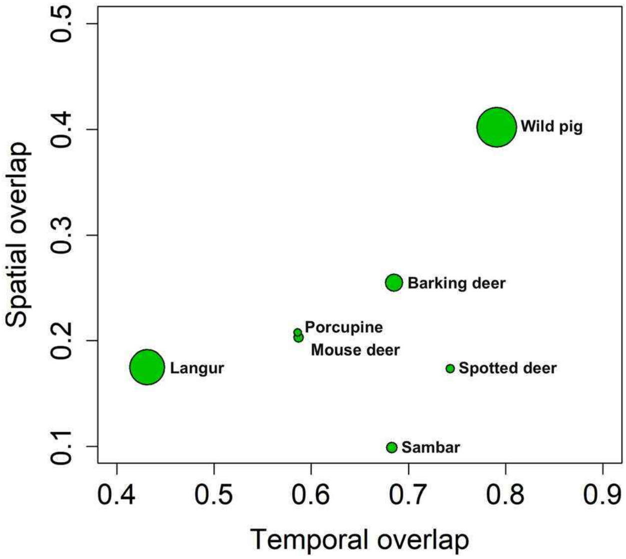

Figure 3: Spatial and temporal overlap of leopard with their prey species plotted together. The size of bubble represents frequency of occurrence (*F*) of prey species in the diet of leopard.

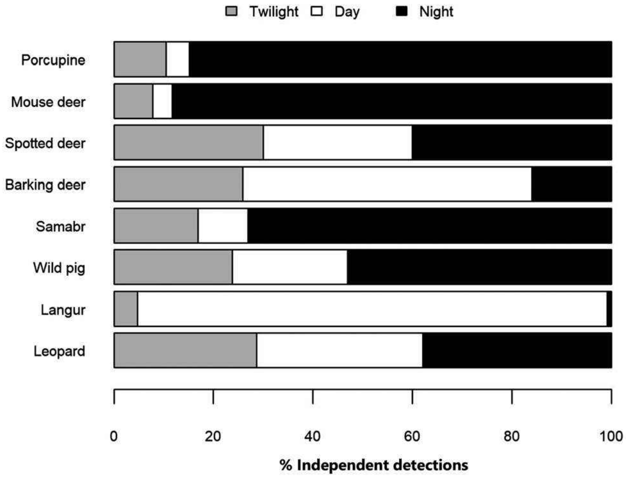

Figure 4: Temporal activity patterns of leopard and their prey represented as the percentage of independent detections in the study area.

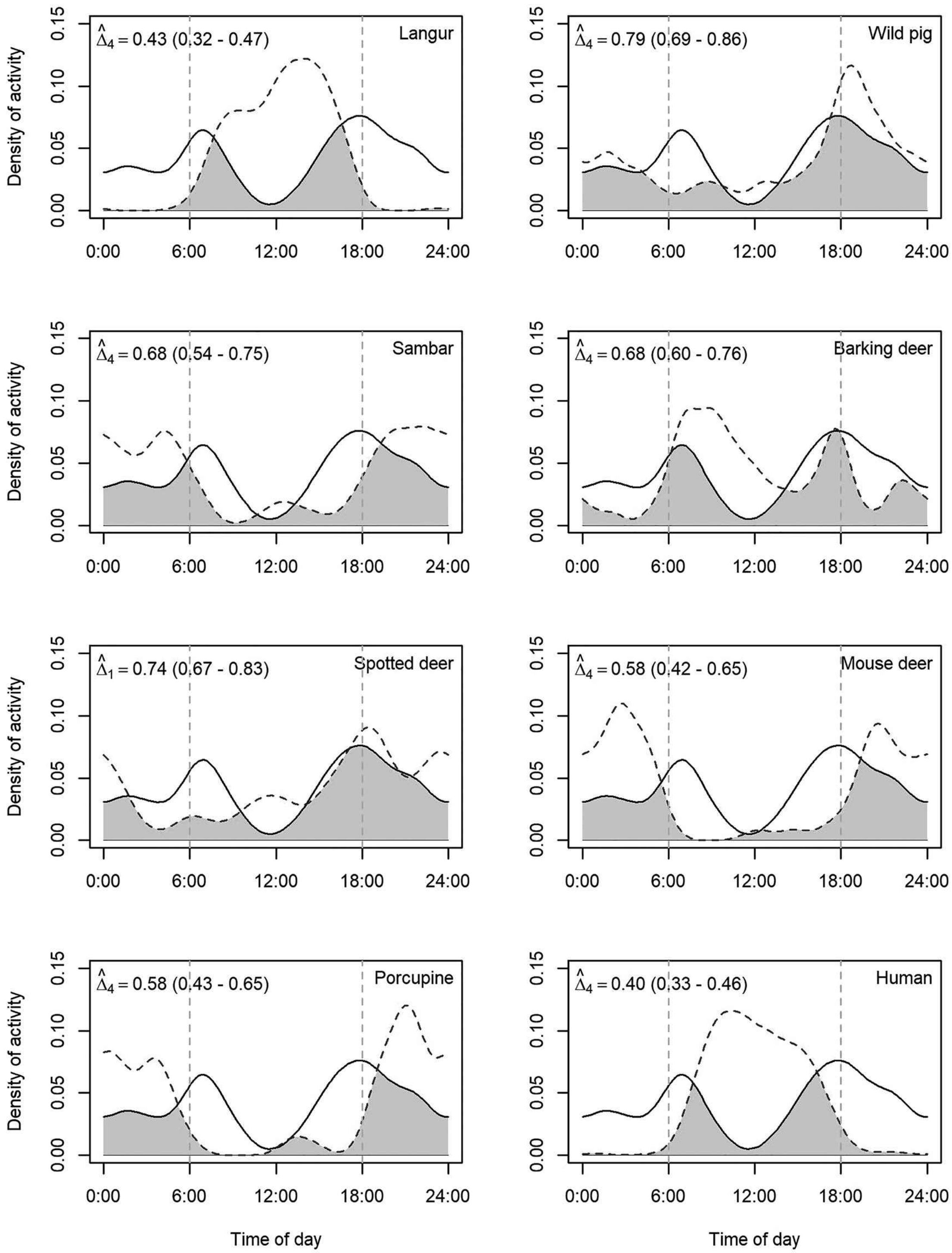

Figure 5: Kernel-density functions of leopard, prey species and human. The overlap coefficient is the area under the kernel-density functions of the two density estimates, as indicated in the shaded area in each plot. The estimate overlap is indicated in each plot, with 95% bootstrap confidence interval in parentheses. The solid line represents the activity of leopard density curve, and the dashed line indicates the activity density curve of the prey species being compared. The vertical dashed lines indicate the approximate time of sunrise and sunset during the study period in the study localities.

4 Discussion

4.1 Diet of leopard

Several studies have shown that leopards have a broader ecological niche; thus, they can exploit a wide range of resources, from small rodents to large ungulates (Hayward et al. 2006). Leopards are morphologically adapted to kill large prey, but they prefer prey species ranging from 10 to 40 kg with an optimum weight of 23 kg (Hayward et al. 2006). In line with studies and our predictions, the present study showed that the leopard consumed more of medium-sized prey species. Furthermore, the wild pig was the most important prey in the frequency of occurrence and relative biomass consumed. The wild pig is a relatively aggressive and dangerous prey for leopards (Eisenberg and Lockhart 1972; Yang et al. 2018), which may account for their status as non-preferred prey in several studies (Hayward et al. 2006). We assumed that leopards might avoid adult wild boar and preferred sub-adult individuals to minimize predation difficulties (Karanth and Sunquist 1995; Sugimoto et al. 2016). Wild boar preference may be a result of a prey-switching strategy (Ghouddousi et al. 2017) of the leopard, likely due to the low densities of other ungulate species in the study area (Upadhyay et al. 2019). After barking deer, a high number of wild pigs were photo-captured in spatial and temporal scales in our study area. Therefore, frequency of wild pig predation in the present study could be attributed to the abundance and wide distribution of wild pig across the study area. Similar in Golestan National Park, Iran showed that wild pig was the most dominant prey in leopard diet due to their high numbers (Ghouddousi et al. 2017).

Common langurs are the second most dominant prey species of leopards in our study area. Basak et al. (2020) reported that common langurs are the prime prey species in the leopard diet in the Udanti Sitanadi tiger reserve and the Bhoramdeo wildlife sanctuary of central India. Five primates species were the most consumed prey taxon in the diet of leopards in the Mahale Mountains National Park, Tanzania (Nakazawa 2019). Our camera trap data showed that common langurs spend a considerable amount of time during the day on the ground; and diurnal hunting for common langurs by leopards was common in Nagarahole National Park, India (Karanth and Sunquist 2000). Radio-tracking data showed that leopards preyed on monkeys on the ground during the daytime in the Taï forest in Ivory Coast (Zuberbühler and Jenny 2002). Unlike other large carnivores, leopards are good climbers and able to hunt arboreal prey like common langurs (Hayward et al. 2006). Cowlishaw (1994) reported that leopard hunt baboons (*Papio* species) actively in Africa. In Huai Kha Khaeng Wildlife Sanctuary, Thailand, barking deer and primates were the first and second most frequent prey, respectively, in the leopards' diet (Rabinowitz 1989). Rabinowitz (1989) and Grassman (1999) reported that primates were at greater risk of predation from the predators due to open canopy in the dry deciduous forest habitat, which often forced them to use ground rather than moving quickly through the canopy. Several studies reported spotted deer is the most consumed prey species of leopard (Hayward et al. 2006). However, the low occurrence of spotted deer hair in leopard scats is probably due to the infrequent predation of spotted deer by leopards, given the extremely low abundance of this species in our study area. The presence of Indian hare, Rhesus macaque, Indian grey mongoose and Indian giant squirrel hair in leopard scats is likely to result from occasional predation on these species.

4.2 Spatiotemporal activity pattern of leopard and prey

The diet spectrum of leopards in our study area was comparable with that previously described from Sariska and Mudumalai tiger reserve in India (Mondal et al. 2011; Ramesh et al. 2012b). Comparatively broader prey spectrum in leopard has been observed in the moist deciduous forest of Dudhuwa National Park in India by Ahmed and Khan (2008) (*n* = 20 species) and in African tropical forest by Henschel et al. (2005) (*n* = 30 species) and Bodendorfer et al. (2006) (*n* = 37 species). Leopards inhabit diverse habitat types of varying altitudes, temperatures and rainfall regimes (Stein et al. 2016). To effectively used prey assemblages in these different ecosystems, a predator needs considerable behavioural plasticity. Leopards showed cathemeral activity pattern, being mostly active during dusk and dawn and least active in the middle of the day in our study area. Our finding was similar to the activity reported in both India and the other regions of Southeast Asia (Can et al. 2020; Chaudhary et al. 2020; Lamichhane et al. 2019; Ramesh et al. 2012a) but contrasted with that of leopards in China (Yang et al. 2018), where Amur leopards showed a strong diurnal pattern. Cathemeral behaviour of predator increases the probability of encounter with a wide variety of prey. It might be beneficial for a generalist carnivore like the leopards, which has a broad dietary spectrum (Yang et al. 2018). In general, leopard activity can be affected by the presence of dominant predators (such as tiger and lion), the activity of its prey, and anthropogenic disturbances (Chaudhary et al. 2020; Ramesh et al. 2012a).

We photo captured the tiger only once in the study area, which suggests that leopard activity may not be affected by the tiger in the study area.

Leopard exhibited low spatial co-occurrence and overlap with their main prey in the study area. This can be discussed in the light of various human disturbances in the study area. Our study demonstrated low spatiotemporal overlap between leopards and humans. In the study area, frequent human presence was observed, engaging in different activities such as livestock grazing and forest produce collection and logging. Although leopard is characterized by great ecological plasticity and occurs in landscapes dominated by anthropogenic activities (Athreya et al. 2013; Hayward et al. 2006), several studies have reported that human disturbance was the most negative influential factor to habitat use and abundance of leopards (Carter et al. 2015; Ngoprasert et al. 2007). Amur leopards keep away from human and livestock use areas (Yang et al. 2018). Havmøller et al. (2019) also indicated that leopards change their spatial distribution response to human disturbances.

Leopard is a solitary ambush hunter. It has lower encounter rates with prey in comparison with chasing hunters. They need dense vegetation to hide and stalk or wait for prey. They spend more time in stalking than searching for prey (Hirt et al. 2020). Therefore, leopards and their preys' encounter depends more on the preys' activity than the leopard. Similar to our prediction, leopards showed substantial temporal overlaps with their main preys, such as wild pig, sambar and barking deer in the study area. Activity overlap may increase their foraging success (Laundré et al. 2010). Our results are consistent with previous studies on the temporal overlap between leopards and their prey (Can et al. 2020; Carter et al. 2015; Jenny and Zuberbühler 2005; Lamichhane et al. 2019). High overlap of leopard temporal activity with wild pig and sambar was recorded in Mudumalai Tiger Reserve and Gir National Park, India (Chaudhary et al. 2020; Ramesh et al. 2012a). However, ungulate species in tropical rainforests in Malaysia exhibit low temporal overlap with leopards (Pudyatmoko 2019; Ross et al. 2013). The low spatiotemporal overlap between leopards and common langurs suggests avoidance by this prey species; however, this pattern must be taken with caution due to primates' arboreality nature, which affects the detection probability (Wearn et al. 2013).

Animal detections require careful consideration (Wearn et al. 2013). Our camera traps height and placement targeted large predators and their prey, especially large and medium-sized ungulates, which may prefer trails as travel routes. It might affect the detection probability of small-bodied mouse deer and arboreal common langur. It has also been reported that larger animals trigger camera traps with a higher probability than small species (Rowcliffe et al. 2011). Therefore, setting camera traps along roads and large trails to detect animals undermine success contrary to the camera trap station's random placement (Ross et al. 2013; Wearn et al. 2013).

5 Conclusion

Despite the methodological caveats mentioned above, camera traps are useful to study spatio-temporal activity patterns of the animal. Our study provides insight into leopards' diet and behavioural ecology in a high human disturbance area with other large predators' absence. Several studies found that leopards exhibit spatiotemporal habitat use and dietary shifts in the presence of a dominant predator such as tigers (Carter et al. 2015; Harihar et al. 2011; Kafley et al. 2019). Leopards used human-influenced forest fringe habitats where they persisted with low prey abundance and domestic prey (Carter et al. 2015; Harihar et al. 2011). Furthermore, Carter et al. (2015) reported that leopards spatially avoided tigers but were not displaced from human activity in Chitwan National Park, Nepal. In our study area, leopards' spatiotemporal activity pattern appears to be determined primarily by "bottom-up" forces and human activity when the presence of a dominant predator such as tiger is not a limiting factor, like those of many apex predators (Elbroch and Kusler 2018; Steinmetz et al. 2013). Our study's findings contribute to understanding the relationship between leopards and their prey and may have implications for the conservation of this apex predator.

Research ethics: Permissions to conduct field research were obtained from the State Forest Department of Odisha under the Guideline for Scientific Research in Protected Areas, Ministry of Environment and Forests, Government of India. This research did not involve handling of animals and otherwise abided by the Govt. of India guidelines on ethical standards.

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References

Ackerman, B.B., Lindzey, F.G., and Hemker, T.P. (1984). Cougar food habits in southern Utah. J. Wildl. Manage 48: 147–155.

Ahmed, K. and Khan, J.A. (2008). Food habits of leopard in tropical moist deciduous forest of Dudhwa National Park, Uttar Pradesh, India. Int. J. Ecol. Environ. Sci. 34: 141–147.

Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J., and Karanth, K.U. (2013). Big cats in our backyards: persistence of large carnivores in a human dominated landscape in India. PLoS One 8: e57872.

Bahuguna, A., Sahajpal, V., Goyal, S.P., Mukherjee, S.K., and Thakur, V. (2010). *Species identification from guard hair of selected Indian mammals: a reference guide*. Wildlife Institute of India, Dehradun, India.

Baliarsingh, B.K., Kosygin, L., Swain, S.K., and Nayak, A.K. (2013). Species diversity and habitat characteristics of freshwater fishes in the Similipal Biosphere Reserve, Odisha with some new records. Biol. Forum 5: 64–70.

Basak, K., Ahmed, M., Suraj, M., Readdy, B.V., Yadav, O.P., and Mondal, K. (2020). Diet ecology of tigers and leopards in Chhattisgarh, central India. J. Threat. Taxa 12: 15289–15300.

Bodendorfer, T., Hoppe-Dominik, B., Fischer, F., and Linsenmair, K.E. (2006). Prey of the leopard (*Panthera pardus*) and the lion (*Panthera leo*) in the Comoé and Marahoué National Parks, Côte d'Ivoire, West Africa. Mammalia 70: 231–246.

Can, Ö.E., Yadav, B.P., Johnson, P.J., Ross, J., D'Cruze, N., and Macdonald, D.W. (2020). Factors affecting the occurrence and activity of clouded leopards, common leopards and leopard cats in the Himalayas. Biodivers. Conserv. 29: 839–851.

Carter, N., Jancy, M., Gurung, B., and Liu, J. (2015). Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. Glob. Ecol. Conserv. 3: 149–162.

Chakraborty, R., Chakraborty, S., and De, J.K. (1999). Identification of dorsal guard hairs of the species of Indian lesser cats (Carnivora: Felidae). Mammalia 63: 93–104.

Chaudhary, R., Zehra, N., Musavi, A., and Khan, J.A. (2020). Spatio-temporal partitioning and coexistence between leopard (*Panthera pardus fusca*) and Asiatic lion (*Panthera leo persica*) in Gir protected area, Gujarat, India. PLoS ONE 15: e0229045.

Cowlishaw, G. (1994). Vulnerability to predation in baboon populations. Behaviour 131: 293–304.

Dash, M. and Behera, B. (2018). Biodiversity conservation, relocation and socio-economic consequences: a case study of Similipal Tiger Reserve, India. Land Use Policy 78: 327–337.

De, J.K., Chakraborty, S., and Chakraborty, R. (1998). Identification of dorsal guard hairs of five Indian species of mongoose, *Herpestes* Illiger (Mammalia: Carnivora). Mammalia 62: 285–296.

Delibes-Mateos, M., Díaz-Ruiz, F., Caro, J., and Ferreras, P. (2014). Activity patterns of the vulnerable guina (*Leopardus guigna*) and its main prey in the Valdivian rainforest of southern Chile. Mamm. Biol. 79: 393–397.

Dou, H., Yang, H., Smith, J.L.D., Feng, L., Wang, T., and Ge, J. (2019). Prey selection of Amur tigers in relation to the spatiotemporal overlap with prey across the Sino–Russian border. Wildl. Biol. 2019: 1–11.

Edgaonkar, A. and Chellam, R. (2002). Food habit of the leopard, *panthera pardus* in the Sanjay Gaandhi National Park, Maharastra, India. Mammalia 66: 353–360.

Eisenberg, J.F. and Lockhart, M. (1972). An ecological reconnaissance of Wilpattu National Park, Ceylon. Smiths. Contrib. Zool 101: 1–118.

Elbroch, L.M. and Kusler, A. (2018). Are pumas subordinate carnivores, and does it matter? PeerJ 6: e4293.

Eriksen, A., Wabakken, P., Zimmermann, B., Andreassen, H.P., Arnemo, J.M., Gundersen, H., Liberg, O., Linnell, J., Milner, J.M., Pedersen, H.C., et al. (2011). Activity patterns of predator and prey: a simultaneous study of GPS-collared wolves and moose. Anim. Behav. 81: 423–431.

Foster, V.C., Sarmento, P., Sollmann, R., Tôrres, N., Jácomo, A.T., Negrões, N., Fonseca, C., and Silveira, L. (2013). Jaguar and puma activity patterns and predator-prey interactions in four Brazilian biomes. Biotropica 45: 373–379.

Ghoddousi, A., Soofi, M., Hamidi, A., Lumetsberger, T., Egli, L., Ashayeri, S., Khorozyan, I.H., Kiabi, B., and Waltert, M. (2017). When pork is not on the menu: assessing trophic competition between large carnivores and poachers. Biol. Conserv. 209: 223–229.

Gotelli, N.J. and Ellison, A.M. (2013). EcoSimR 1.00, Available at: http://www.uvm.edu/~ngotelli/EcoSim/EcoSim.html.

Grassman, L.I. (1999). Ecology and behavior of the Indochinese leopard in Kaeng Krachan National Park, Thailand. Nat. Hist. Bull. Siam Soc. 47: 77–93.

Griffith, D.M., Veech, J.A., and Marsh, C.J. (2016). Cooccur: probabilistic species co-occurrence analysis in R. J. Stat. Softw 69: 1–17.

Harihar, A., Pandav, B., and Goyal, S.P. (2011). Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. J. Appl. Ecol. 48: 806–814.

Harmsen, B.J., Foster, R.J., Silver, S.C., Ostro, L.E., and Doncaster, C.P. (2011). Jaguar and puma activity patterns in relation to their main prey. Mamm. Biol. 76: 320–324.

Havmøller, R.W., Tenan, S., Scharff, N., and Rovero, F. (2019). Reserve size and anthropogenic disturbance affect the density of an African leopard (*Panthera pardus*) meta-population. PLoS One 14: e0209541.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., and Kerley, G.I.H. (2006). Prey preferences of the leopard (*Panthera pardus*). J. Zool. 270: 298–313.

Henschel, P., Abernethy, K.A., and White, L.J.T. (2005). Leopard food habits in the Lopé National Park, Gabon, Central Africa. Afr. J. Ecol. 43: 21–28.

Hirt, M.R., Tucker, M., Müller, T., Rosenbaum, B., and Brose, U. (2020). Rethinking trophic niches: speed and body mass colimit prey space of mammalian predators. Ecol. Evol. 10: 7094–7105.

Ivlev, V.S. (1961). *Experimental ecology of the feeding of fishes*. Yale University Press, New Haven, CI.

Jhala, Y.V., Qureshi, Q., and Gopal, R. (2015). *The status of tigers, copredators & prey in India 2014*. National Tiger Conservation Authority, New Delhi & Wildlife Institute of India, Dehradun.

Jenny, D. and Zuberbühler, K. (2005). Hunting behaviour in West African forest leopards. Afr. J. Ecol. 43: 197e200.

Johnsingh, A.J.T. (1992). Prey selection in three sympatric carnivores in Bandipur. Mammalia 56: 517–526.

Kafley, H., Lamichhane, B.R., Maharjan, R., Khadka, M., Bhattarai, N., and Gompper, M.E. (2019). Tiger and leopard co-occurrence: intraguild interactions in response to human and livestock disturbance. Basic Appl. Ecol. 40: 78–89.

Karanth, K.U. and Sunquist, M.E. (1995). Prey selection by tiger, leopard and dhole in tropical forests. J. Anim. Ecol. 64: 439–450.

Karanth, K.U. and Sunquist, M.E. (2000). Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. J. Zool. 250: 255–265.

Karanth, K.U., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R., and Kumar, N.S. (2017). Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. Proc. R. Soc. B 284: 20161860.

Kuhn, R.A. and Meyer, W. (2010). Comparative hair structure in the Lutrinae (Carnivora: Mustelidae). Mammalia 74: 291–303.

Lamichhane, B.R., Leirs, H., Persoon, G.A., Subedi, N., Dhakal, M., Oli, B.N., Reynaert, S., Sluydts, V., Pokheral, C.P., Poudyal, L.P., et al. (2019). Factors associated with co-occurrence of large carnivores in a human-dominated landscape. Biodivers. Conserv. 28: 1473–1491.

Laundré, J.W., Hernandez, L. and Ripple, W.J. (2010). The landscape of fear: ecological implications of being afraid. Open Ecol. J. 3: 1–7.

Linkie, M. and Ridout, M.S. (2011). Assessing tiger–prey interactions in Sumatran rainforests. J. Zool. 284: 224–229.

Marinho, P.H., Bezerra, D., Antongiovanni, M., and Fonseca, C.R. (2018). Activity patterns of the threatened northern tiger cat *Leopardus tigrinus* and its potential prey in a Brazilian dry tropical forest. Mamm. Biol. 89: 30–36.

Meredith, M. and Ridout, M. (2017). Overview of the overlap package. R project.

Mishra, R.K., Nayak, A.K., Sahu, H.K., and Palei, H.S. (2016). *Ecology of similipal biosphere reserve*. Daya Publishing House, Astral International Pvt. Ltd., New Delhi.

Mondal, K., Gupta, S., Qureshi, Q., and Sankar, K. (2011). Prey selection and food habits of leopard (*Panthera pardus fusca*) in Sariska Tiger Reserve, Rajasthan, India. Mammalia 75: 201–205.

Nair, M.V. (2007). Butterflies of Similipal Tiger Reserve: a preliminary study on species diversity, species composition and habitat preference. e-planet 5: 76–81.

Nakazawa, N. (2019). Primates are an important food resource for leopards (*Panthera pardus*) in Mahale, Tanzania. Afr. J. Ecol. 00: 1–10.

Ngoprasert, D., Lynam, A.J., and Gale, G.A. (2007). Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. Oryx 41: 343–351.

O'Brien, T., Kinnaird, M.F., and Wibisono, H.T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Anim. Conserv. 6: 131–139.

Ordiz, A., Bischof, R., and Swenson, J.E. (2013). Saving large carnivores, but losing the apex predator? Biol. Conserv. 168: 128–133.

Palei, H.S., Pradhan, T., Sahu, H.K., and Nayak, A.K. (2016a). Estimating mammalian abundance using camera traps in the tropical forest of Similipal Tiger Reserve, Odisha, India. Proc. Zool. Soc. 69: 181–188.

Palei, H.S., Sahu, H.K., and Nayak, A.K. (2016b). Ungulate densities and biomass in the tropical moist deciduous forest of Similipal Tiger Reserve, India. Natl. Acad. Sci. Lett. 39: 255–258.

Pianka, E.R. (1973). The structure of lizard communities. Annu. Rev. Ecol. Syst. 4: 53–74.

Porfirio, G., Foster, V.C., Fonseca, C., and Sarmento, P. (2016). Activity patterns of ocelots and their potential prey in the Brazilian Pantanal. Mamm. Biol. 81: 511–517.

Pudyatmoko, S. (2019). Spatiotemporal inter-predator and predator–prey interactions of mammalian species in a tropical savanna and deciduous forest in Indonesia. Mammal Res. 64: 191–202.

Rabinowitz, A. (1989). The density and behaviour of large cats in a dry tropical forest mosaic in Huai Kha Khaeng Wildlife Sanctuary, Thailand. Nat. Hist. Bull. Siam Soc. 37: 235–251.

Ramesh, T., Kalle, R., Sankar, K., and Qureshi, Q. (2012a). Spatio-temporal partitioning among large carnivores in relation to major prey species in Western Ghats. J. Zool. 287: 269–275.

Ramesh, T., Kalle, R., Sankar, K., and Qureshi, Q. (2012b). Dietary partitioning in sympatric large carnivores in a tropical forest of Western Ghats, India. Mamm. Study 37: 313–321.

Rich, L.N., Miller, D.A.W., Robinson, H.S., McNutt, J.W., and Kelly, M.J. (2017). Carnivore distributions in Botswana are shaped by resource availability and intraguild species. J. Zool. 303: 90–98.

Ridout, M.S. and Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. 14: 322–337.

Ripple, W.J., Wirsing, A.J., Wilmers, C.C., and Letnic, M. (2013). Widespread mesopredator effect after wolf extirpation. Biol. Conserv. 160: 70–79.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., et al. (2014). Status and ecological effects of the world's largest carnivores. Science 343: 1241484.

Ross, J., Hearn, A.J., Johnson, P.J., and Macdonald, D.W. (2013). Activity patterns and temporal avoidance by prey in response to Sunda clouded leopard predation risk. J. Zool. 290: 96–106.

Rowcliffe, J.M. and Carbone, C. (2008). Surveys using camera traps: are we looking to a brighter future? Anim. Conserv. 11: 185–186.

Rowcliffe, J.M., Carbone, C., Jansen, P., Kays, R., and Kranstauber, B. (2011). Quantifying the sensitivity of camera traps: An adapted distance sampling approach. Meth. Ecol. Evol. 2: 464–476.

Saxena, H.O. and Brahmam, M. (1989). *The flora of Similipahar, Orissa*. Regional Research Laboratory, Bhubaneswar.

Stein, A.B., Athreya, V., Gerngross, P., Balme, G., Henschel, P., Karanth, U., Miquelle, D., Rostro-Garcia, S., Kamler, J.F., Laguardia, A., et al. (2016). *Panthera pardus* (errata version published in 2016). The IUCN Red List of Threatened Species 2016: e.T15954A102421779, https://doi.org/10.2305/IUCN.UK.20161.RLTS.T15954A50659089.en (Downloaded 30 March 2020).

Steinmetz, R., Seuaturien, N., and Chutipong, W. (2013). Tigers, leopards, and dholes in a half-empty forest: assessing species interactions in a guild of threatened carnivores. Biol. Conserv. 163: 68–78.

Stephens, P.A., Pettorelli, N., Barlow, J., Whittingham, M.J., and Cadotte, M.W. (2015). Management by proxy? The use of indices in applied ecology. J. Appl. Ecol. 52: 1–6.

Sugimoto, T., Aramilev, V.V., Nagata, J., and McCullough, D.R. (2016). Winter food habits of sympatric carnivores, Amur tigers and Far Eastern leopards, in the Russian Far East. Mamm. Biol. 81: 214–218.

Surkova, E.N., Vinarskaya-Korallo, N.P., Vinarski, M.V., and Mescht, L.V.D. (2018). Body size distribution in flea communities harboured by Siberian small mammals as affected by host species, host sex and scale: scale matters the most. Evol. Ecol. 32: 643–662.

Upadhyay, H.S., Behera, S., Dutta, S.K., Sahu, H.K., and Sethy, J. (2019). A viable tiger population in Similipal Tiger Reserve, India? Calculating if the ungulate prey base is limiting. Wildl. Biol. 2019: 1–7.

Veech, J.A. (2013). A probabilistic model for analysing species co-occurrence. Glob. Ecol. Biogeogr. 22: 252–260.

Wearn, O.R., Rowcliffe, J.M., Carbone, C., Bernard, H., and Ewers, R.M. (2013). Assessing the status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. PLoS ONE 8: e77598.

Wikramanayake, E.D., Dinerstein, E., Robinson, J.G., Karanth, K.U., Rabinowitz, A., Olson, D., Mathew, T., Hedao, P., Conner, M., Hemley, G., et al. (1998). An ecology-based method for defining priorities for large mammal conservation: the tiger as case study. Conserv. Biol. 12: 865–878.

Yang, Y., Zhao, X., Han, B., Wang, B., Mou, B., Ge, J., and Feng, L. (2018). Spatiotemporal patterns of Amur leopards in northeast China: influence of tigers, prey, and humans. Mamm. Biol. 92: 120–128.

Zuberbühler, K. and Jenny, D. (2002). Leopard predation and primate evolution. J. Hum. Evol. 43: 873–886.