Spatio-temporal patterns of co-occurrence of tigers and leopards within a protected area in central India

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Abstract. The global decline of large carnivore populations warrants scientific insights into intraguild relationships. Patterns of co-occurrence among sympatric predators are governed by their density, distribution, diet, activity overlaps, and behavioural strategies. Tigers are sympatric with leopards across their distribution range, overlap substantially in their diet, and are both nocturnal. The subdominant leopard is believed to co-exist with tigers via several mechanisms like spatial segregation, temporal avoidance, and differential prey selection. Investigation of spatio-temporal patterns of co-occurrence of tigers and leopards can provide insights on mechanisms that permit coexistence. We used camera trap-based photo captures of tigers and leopards in prey-rich (58.15 ± 10.61 ungulates per km^2) Pench Tiger Reserve to determine their spatio-temporal patterns of co-occurrence. Spatially explicit density estimates of tigers were approximately 5 per 100 km^2 and leopards were approximately 4.5 per 100 km^2 and remained stable over the years. This implies that both these co-predators are likely to attain carrying capacity within the study area. Areas with high tiger density had lower leopard density. Quantile regression analysis between tiger and leopard density at 2×2 km grid showed that leopard density had a parabolic relationship with tiger density, initially increasing with tigers ($\beta = 0.393$; $p = 0.001$), stable at medium tiger density ($\beta = 0.13$ and $p = 0.15$), and declining at high tiger densities ($\beta = -0.37$ and $p < 0.001$). Both tigers and leopards were crepuscular in nature with no temporal segregation ($\Delta = 89\%$). Time lag of consecutive leopard photograph after a tiger capture ranged between 0.002 to 36.29 d. Leopard use of trails was not related to use by tigers. Our results suggest that leopards adjust their usage of space at fine scales to avoid confrontations with tigers. We also observed high temporal overlap and no spatio-temporal segregation between tigers and leopards, despite the two predators being nocturnal and having similar prey choices. The availability of ample prey within the study area is likely to be the driving factor of the co-occurrence of tigers and leopards within this dry deciduous habitat of central India.

1 Introduction

Large carnivores at the apex of the trophic pyramid inherently occur at low densities, compete with human interests, and are therefore one of the most difficult taxa to conserve (Cardillo et al., 2004; Ripple et al., 2014). Large carnivores play a crucial role in structuring ecosystems and form an important element of intact functional systems (Linnell and Strand, 2000; Ripple et al., 2001; Durant et al., 2010). Populations of many large carnivores are restricted to protected areas (PAs) that are of limited size (Jhala et al., 2020). On an average, the PAs of India which harbour approximately 70 % of the world's extant tiger population (Jhala et al., 2015) have a size of 393 km^2 embedded in a matrix of human-dominated land-use pattern (Bisht et al., 2019). Consequently, few parks

have demographically viable carnivore populations (Jhala et al., 2020), but high prey densities within the PAs have enabled to harbour high densities of large- and medium-bodied predators (Bisht et al., 2019). However, inter-carnivore interactions can further become a limiting factor for their survival (Creel, 2001; Caro and Stoner, 2003; Durant et al., 2010). In multi-large carnivore systems, understanding of mechanisms that permit their coexistence among competing carnivores in time and space (Miller et al., 2018) is essential for understanding the population dynamics of the target species and the factors which influence the same (Estes et al., 2011; Wilman et al., 2014; Di Minin et al., 2016).

Species assemblage in a system is governed by niche partitioning between different species (Begon et al., 1990; Mayhew 2006). Different factors such as habitat requirements, body size, behavioural adaptations, and density determine the way interspecific interactions will take place among sympatric species (Thompson, 1988). Interspecific interactions, in turn, influence population growth rate and species distribution range (Svenning et al., 2014). Different types of interspecific interactions among competing predators can range from coexistence to intraguild killing. Coexistence between competing predators can be achieved by differential usage of non-limiting resources, e.g. preferential predation of deer and young elk by coyotes in the presence of wolves (Paquet, 1992) and predation of prey of poorer health condition by leopards in the presence of tigers (Majumder et al., 2013). Behavioural adaptations like segregation on a spatial scale, e.g. spatial avoidance of coyotes by red foxes (Voigt and Earle, 1983), and temporal and/or spatio-temporal segregation also facilitate amongst interacting carnivores (Kozlowski et al., 2008; Vanak et al., 2013). In the human-dominated landscape of Chitwan, Nepal, tigers and leopards were seen to co-occur by segregating spatially, whereas their temporal overlap was high (Lamichhane et al., 2019). Another study in Chitwan, Nepal, found tiger density to be high in prey-rich areas which also showed lower occupancy of leopards (Kafley et al., 2019). In the absence of the top predator, tigers, in Kuiburi National Park, Thailand, the distribution of subdominant predators, which are leopards and dholes, was primarily governed by prey availability (Steinmetz et al., 2013). The subdominant species has been observed to coexist with the dominant one by investing more energy, including residing in inferior quality habitat or travelling more in the African continent (Caro and Stoner, 2003). Coexistence between clouded leopards and marbled cats was achieved by temporal segregation in Dampa Tiger Reserve, India (Singh and Macdonald, 2017). Diel activity patterns of predators are governed not only by co-predators, but also the activity patterns of prey. While on one hand prey attempt to reduce the risk of predation by reducing temporal overlap with predators, predators aim to maximise their temporal overlap with prey to ensure their hunting success (Lima, 2002). The daily activity pattern of a given prey species is a function of its fundamental niche and local selective forces

like predation pressure, intraguild interactions, and accessibility to resources (Fenn and MacDonald, 1995; Kronfeld-Schor and Dayan, 2008; Monterroso et al., 2013). Predator activity pattern is governed by temporal availability of feeding resources in addition to their fundamental niche and local constraints (Halle, 2000; Lima, 2002; Monterrose et al., 2013). However, not all interactions in nature enable coexistence between competing species. Annual mortality owing to intraguild killing varied from 4 %, where coyotes preyed on martens, to 76 %, where kit foxes were killed by coyotes and red foxes (Palomares and Caro, 1999; Caro and Stoner, 2003; Kozlowski et al., 2008). Another form of competition, kleptoparasitism, where one predator steals the kills from another, is fairly common (Iyengar, 2008; Pereira et al., 2014). In the presence of kleptoparasites like the spotted hyena, the population status of the affected species like African wild dogs dwindles because of alterations in their activity budgets, which may even lead to local extinction of a population (Carbone et al., 1997; Scantlebury et al., 2014; Saggiomo et al., 2017).

A number of studies have looked into the dynamics of carnivore coexistence patterns on a large geographical scale (e.g. Mills et al., 2001; Ritchie and Johnson, 2009; Miller et al., 2018; Prugh and Sivy, 2020). These studies report that large carnivores are responsible for the suppression of smaller predators on a global scale through interspecific interactions (Ritchie and Johnson, 2009; de Oliveira and Pereira, 2014; Prugh and Sivy, 2020). However, the pattern of interactions varied with resource availability, habitat structures, and composition of the predator guild (Ritchie and Johnson, 2009). In addition to this, studies of interspecific interactions at smaller scales are essential, as the fine-scale behavioural adaptations and niche differentiation mechanisms adapted by competing predators in a multi-predator system often fail to emerge at larger scales (Durant, 1998; Durant et al., 2010; Swanson et al., 2016; Farris et al., 2020).

Interactions between tigers (*Pathera tigris* L.) and leopards (*Panthera pardus* L.) are perfectly suited to understand how such mechanisms within a landscape can affect the functioning and structuring of large predator guilds. Tigers are sympatric with leopards across their range of occurrence (Odden et al., 2010). Although the geographical range of tigers has been reduced to more than 90 % over the past 100 years (Dinerstein et al., 2007), they still play their ecological role in several tiger reserves of India (Jhala et al., 2020) and are the apex predator in these systems. Leopards are more prone to intraguild competition and predation by tigers because of their taxonomic relatedness, similar feeding habit, and difference in body size which probably results in avoidance of tigers by leopards to enhance their chances of survival (Polis et al., 1989; Palomares and Caro, 1999; Donadio and Buskirk, 2006). The multiple mechanisms that permit their coexistence have been reported, which vary from differential prey selection between the two carnivores based on prey size class (Johnsingh, 1992; Karanth and Sunquist,

1995, 2000; Majumder et al., 2013) to expanded diet niche of leopards including domestic livestock, small mammals, and birds in the presence of tigers at high density (Odden et al., 2010; Harihar et al., 2011). A number of studies across tigers' extant range have reported that leopards alter their spatial use of habitats (Odden et al., 2010) in addition to low abundance and occupancy in response to presence of tigers (Harihar et al., 2011; Mondal et al., 2012). Subdominant predators may avoid competition by avoiding areas of higher population density of the dominant predator (Sherry, 1979; Karanth et al., 2017). Karanth et al. (2017) also found evidence of behavioural character displacement across the resource availability gradient, as they found variation in the degree of spatial and temporal overlap in different landscapes with variation in prey abundance. However, they also mention that if probabilities of site usage get closer to 1, it can become difficult to detect signs of spatial aggregation or separation. On the other hand, leopards have successfully increased their densities in areas of decreasing tiger density (Kumar et al., 2019). Leopards were also known to change their activity pattern to reduce competition with tigers in the same area (Mondal et al., 2012; Ramesh et al., 2012; Karanth et al., 2017; Li et al., 2018). Hence, it can be said that the interactions between subdominant leopard and dominant tiger and their co-occurrence mechanisms vary from site to site depending on tiger density and prey availability.

With this background, we studied tiger–leopard interactions using long-term camera trap data in Pench Tiger Reserve (PTR) in the state of Madhya Pradesh that is home to the largest tiger (Jhala et al., 2020) and leopard (Jhala et al., 2021) population in India. These two sympatric predators showed a dietary overlap of more than 90 % in PTR with chital (*Axis axis*) as the principal prey (Majumder et al., 2012a). This kind of substantial dietary overlap can effectively result in exploitative interference competition among the predator guild (Creel and Creel, 1996; Hayward et al., 2006). According to the niche complementarity hypothesis, a high degree of overlap in one of the niche components should result in low overlap in at least another niche component (Schoener, 1974; Jimenez, 1996; Lucherini et al., 2009). Hence, given the high dietary overlap among tigers and leopards in the study area (Majumder et al., 2012a), we hypothesise that leopards will occur at lower densities in the regions with high tiger abundance and/or alter their activity pattern to avoid lethal interactions with tigers. We expected relations between tiger and leopards to differ with varying densities of tigers. We hypothesised a parabolic relationship between tiger and leopard densities, i.e. that at low tiger densities, leopards should exhibit an increasing trend with tiger densities; at medium tiger densities, there would be no relation between tiger and leopard densities; while at high tiger densities, leopards would show a declining trend with increasing tiger density.

2   Materials and methods

This study was conducted in Pench Tiger Reserve, Madhya Pradesh, central India. PTR (78°55′ to 79°35′ E and 21°40 to 21°57′ N) has an area of 410 km^2 including Indira Priyadarshini National Park and Pench Mowgli Sanctuary. PTR along with Kanha Tiger Reserve constitutes one of the 11 level I tiger conservation units (TCUs) in India classified by Wikramanayake et al. (1998) (Fig. A1). The adjoining forest tract in north and northeast boundary of Pench provides crucial corridor linkage to Satpura Tiger Reserve, forming an important link between Satpura and Maikal populations of tigers and leopards forming a major source population for these carnivores in central Indian landscape (Jhala et al., 2020, 2021). The home range of tigers in PTR ranges from 19 to 64 km^2 in PTR (Majumder et al., 2012b).

Bio-geographically, PTR is a part of the Deccan Peninsula Central Highlands (Sankar et al., 2013). Major forest types of PTR are tropical moist deciduous forest to slightly moist teak forest and tropical dry deciduous forest. Tropical dry deciduous forest is further classified into dry teak forest and southern dry mixed deciduous forest (Champion and Seth, 1968). Other vegetation types include southern moist mixed deciduous forest and *Boswellia* forest. Annual rainfall ranges from 1300 to 1400 mm in June to September. Other carnivores found here were Asiatic wild dogs (*Cuon alpinus*) which reside within the park and wolves (*Canis lupus*) which usually dwell in fringes. The sloth bear (*Melursus ursinus*) is the only bear species found in this reserve. Wild ungulates include chital (*Axis axis*), sambar (*Rusa unicolor*), gaur (*Bos gaurus*), nilgai (*Boselaphus tragocamelus*), wild pig (*Sus scrofa*), barking deer (*Muntiacus muntjac*), chowsingha (*Tetraceros quadricornis*), chinkara (*Gazella bennetti*), and blackbuck (*Antelope cervicapra*) (Sankar et al., 2013). PTR has one of the highest densities of chital (44–52 individuals per km^2 during the study period) and sambar (5–8 individuals per km^2 during the study period) in India (Jhala et al., 2020; Chatterjee et al., 2022). This makes the study area rich in ungulate prey, which has the potential to sustain high densities of tiger and leopard. A total of 99 villages are located within the "zone of influence" of PTR, harbouring a population of 61 000 individuals mostly comprised by the "Gond" tribe (Sankar et al., 2013). Agriculture is the most prevalent land use pattern outside PTR followed by human settlements and urban centres (Dutta et al., 2016).

We used camera trap-based capture–mark–recapture framework (Karanth and Nichols, 1998) to estimate spatially explicit densities of tigers and leopards (Borchers and Efford, 2008). The natural markings of animals like tigers, leopards, and jaguars are perfectly suited for unique individual identification. In spatially explicit capture–recapture (SECR), the spatial capture history alongside the spatial layout of traps and a mask delineating the maximum space usage of the target population are used to estimate the density (Royle et al., 2013).
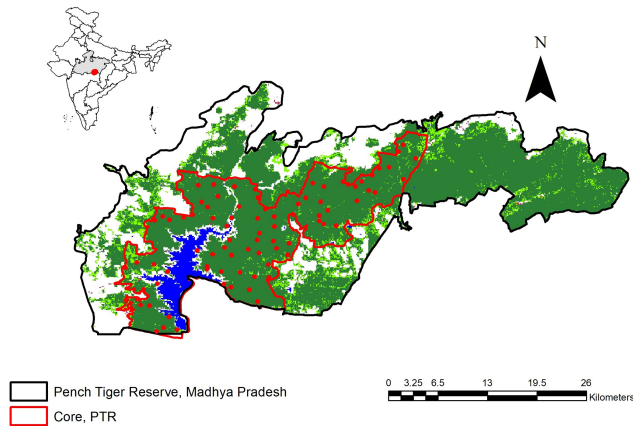
Figure 1. Location of camera trap stations in Pench Tiger Reserve, Madhya Pradesh (2013–2016). Map inset shows the location of Pench Tiger Reserve in India.

2.1   Field methods

The entire study area $(410\,\mathrm{km}^2)$ was systematically sampled by deploying a pair of camera traps within $4\,\mathrm{km}^2$ grids, thereby decreasing the chances of the area remaining unsampled (Fig. 1). The selected locations had the highest capture probability of tigers and leopards. Tigers and leopards do not walk at random but are known to use game trails, dirt roads, and dry riverbeds for commuting and patrolling their territories. Hence, two sided camera traps were deployed at 82 stations after an initial ground survey (of 970 km) for selecting the best locations on such trails and roads to photo capture large carnivores. The same locations were sampled for the entire study period of 3 years (2013–2016). Cameras were placed at the height of 45 cm above ground level facing the trail directly. No olfactory lure was used to attract the target animals to the cameras. Cameras operated during two periods each year (November to October): first, during a 50–55 d block from November to January, and second, a 50–55 d block from January to March. This ensured that the population remained closed for the sampling duration by ensuring no birth, no death, no immigration, and emigration from the target population. The minimum distance between two camera stations varied between 1.5 and 2 km (Sharma and Jhala, 2011). In order to maximise the capture probability, trapping units were properly camouflaged using natural materials like leaves, twigs etc. to reduce the chances of "trap shyness".

2.2   Analytical methods

Individual identification of tiger and leopard was done based on examination of the position, shape of stripes, and rosettes on the flanks (Schaller, 1967; McDougal, 1977; Karanth, 1995; Jhala et al., 2008), limbs, forequarters, and tail (Schaller, 1967; McDougal, 1977; Karanth, 1995). We used individuals which had both flanks, and then the flank

with greater number of individuals were taken into account. Hotspotter (Crall et al., 2013) software was used to assist in the individual identification of leopards. Individuals were classified into different age groups by body characteristics (Sadhu et al., 2017).

A spatial capture history of tigers and leopards that had information on individuals captured and trap locations was prepared from the photo captures obtained from camera traps (Efford, 2011).

2.2.1   Density and distribution pattern

Maximum-likelihood-based spatially explicit capture–recapture framework (MLSECR) (Efford, 2004; Borchers and Efford, 2008) using camera trap data was employed to estimate densities of tigers and leopards for each year separately. SECR density is estimated from two parameters determined from the spatial capture–recapture (i) detection probability $(g0)$ at range centres and (ii) spatial scale of detection (σ) using a homogeneous spatial point process (Efford et al., 2009). The spatial scale of capture probability (σ) is a decreasing function of distance d between the activity centre and the detector. We fitted a half normal function to model σ. Activity centres of individuals are unknown but assumed to follow a Poisson distribution with density D. We defined the state space by using the "suggest.buffer" function in SECR package in R. This function estimates the required buffer width around the camera trapping array by using the spatial movement parameters from the capture recapture information of the data (Efford, 2004).

We modelled $g0$ and σ as (i) constant detection probability $(g0(.), \sigma(.))$ and (ii) inherent heterogeneity in $g0$ and σ as two groups $(g0(h2), \sigma(h2))$. Combined effects of (iii) heterogeneous $g0$ and constant σ along with heterogeneous σ and constant $g0$ $[g0(h2)\,\sigma(.)$ and $g0(.)\sigma(h2)]$ were also modelled (Roy et al., 2016; Kumar et al., 2019). Sunquist and Sunquist (2002) demonstrated that home range size and movement of large cats vary between the sexes, which has the potential to induce variability in the capture probability of individuals (Efford and Mowat, 2014). This latent variability was accounted for by modelling (iii) $g0$ and σ as a function of gender $(g0(\mathrm{sex}), \sigma(\mathrm{sex})$. Due to the long-term data, sex of most tigers and leopards was known from camera trap images; however, for unsexed individuals, the model uses the capture probability of the known gender individuals to allocate unsexed individuals to a gender class using hybrid mixture models. In this model, *pmix* denotes the mixing parameter of two sexes which is used to model the detection function as a two-class mixture. It provided the detection corrected sex ratio of the target species (Kumar et al., 2019). The best model was selected with minimum Akaike information criteria (AICc) values (Burnham and Anderson, 2002). Estimated spatial density of both the species was used to predict the spatial distribution pattern in the study area using ArcMap v. 9.3.1. Although the density surface described by the selected

model is actually the realised capture process unless modelled with habitat covariates (Efford, 2018), the spatial capture process and the density of animals are highly correlated with each other. Hence, it can be treated as a density surface. Data processing was carried out in MS Excel v. 2007 and analyses were carried out using the "secr" package (Efford, 2015) in the programme R v. 3.1.3. Individuals more than 1 year old were taken into account for density estimation, as high mortality rate and low capture probability of younger individuals can possibly reduce the robustness of the estimates (Karanth and Nichols, 1998; Sadhu et al., 2017).

We extracted averaged values of the normalised difference vegetation index (NDVI) and averaged relative abundance index (RAI) values of chital, sambar, wild pig, leopard, and tiger densities at 2×2 km grids. RAI was calculated as capture rate of target animals per 100 trap nights. Subsequently, relationships between NDVI and prey RAI were explored with tiger and leopard densities and between tiger and leopard densities. As we hypothesised a parabolic relationship between tiger and leopard density, we used a quantile regression to obtain estimates of the quantiles of leopard density as a function of tiger density because it does not need to assume a parametric form of the error distribution (Koenker and Bassett, 1978; Cade and Noon, 2003; Koenker, 2005). In case of quantile regression, the usual single-mean function of linear or non-linear regression is substituted by a family of functions across all or a part of quantiles on the interval of 0 to 1. In this case, we divided the data into four intervals (0.25, 0.5, 0.75, and 0.95). This in turn provides a holistic picture of change in all parts of the distribution of the response variable with respect to the predictor variable (Cade et al., 2008).

2.2.2 Activity peaks and temporal overlap

In order to check whether leopards alter their activity pattern to avoid tigers, camera trap-based photographs were used to evaluate their activity peaks and extent of temporal overlap with tigers. ExifPro v.2.1 was used to extract the temporal information of photo captures of tigers and leopards, as all the photographs from the detectors were stamped with date and time of capture. We consider a photo capture as an independent event if the same individual tiger or leopard was photo-captured at the same location after an interval of 30 min. A von Mises kernel density estimate corresponding to circular distribution function (Ridout and Linkie, 2009) was used to generate the activity pattern for both carnivores. Activity peaks were identified based on the maximum number of captures obtained at a specific time period (Linkie and Ridout, 2011; Foster et al., 2013). The coefficient of overlap (Δ) in activity between the two carnivores was estimated as the overlap area under the density curve. We calculated the extent of temporal overlap from the coefficient of overlap and its 95% confidence interval using 10 000 bootstrap samples (Meredith and Ridout, 2014). The extent of overlap varies from 0 (no overlap) to 1 (100 % overlap, identical activity
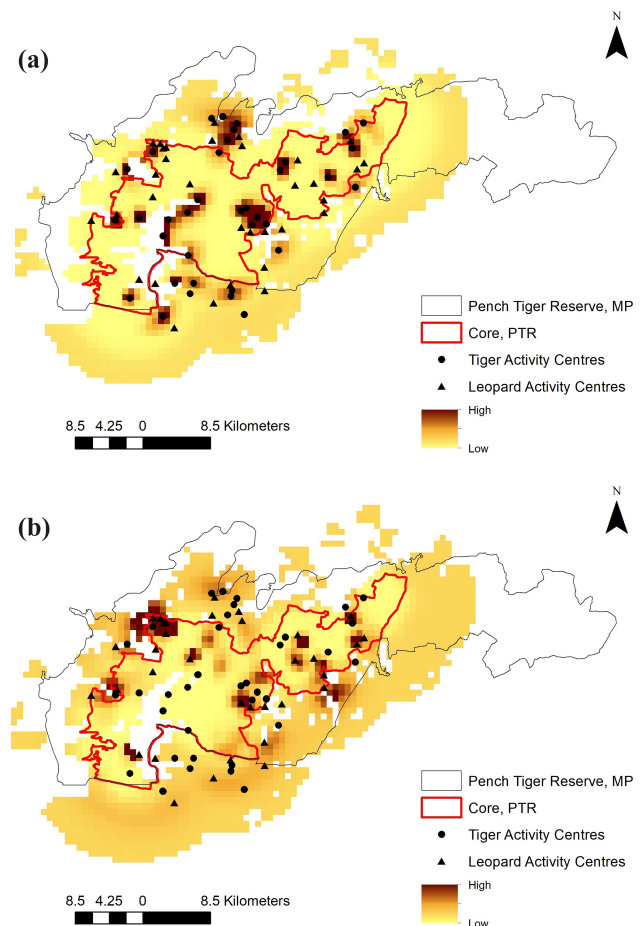
Figure 2. Spatial distribution pattern mapped in terms of realised capture process of **(a)** tigers and **(b)** leopards in the intensive study area.

pattern) (Ridout and Linkie, 2009). We estimated temporal overlap between tigers and leopards at high, medium, and low levels of tiger density. For this, we divided the study area into three tiger density categories based on the encounter rate of tigers per 100 trap nights: high (6.36 to 32.73), medium (3.64 to 5.45), and low (0.9 to 2.72), and estimated the temporal overlap in these three categories. This classification was done based on different quartiles, where low was the lowest quartile, medium was the second quartile, and high was the third and fourth quartiles of the encounter rate. We also estimated their extent of overlap in each year. Additionally, we wanted to check the extent of temporal overlap between these two predators and their preferred prey species. So, we estimated the temporal overlap between these two sympatric predators and their principal prey, which are chitals, sambars, and wild pigs, following the same method. Statistical analysis was done in the "overlap" package (Meredith and Ridout, 2014) in R (v. 3.1.3).
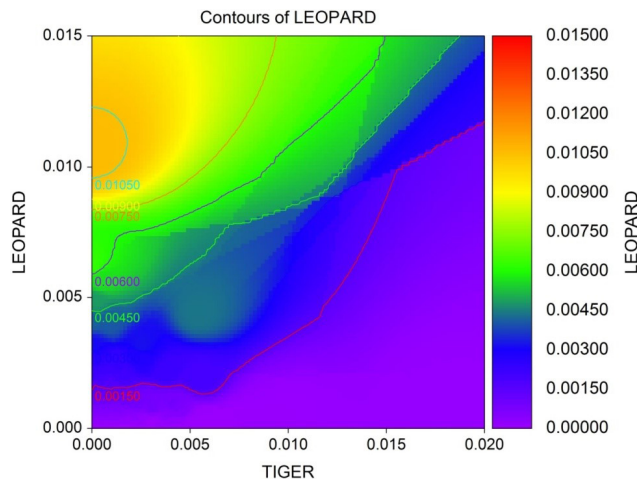
Figure 3. Diagrammatic representation of leopard density contours against tiger density areas. Plotted density contours of leopards against that of tigers show that density of leopards declines with increase in the density of tigers.

2.2.3 Temporal spacing of detections at shared camera sites

Temporal information of photo captures of tigers and leopards at each camera station was transformed to Julian format for analysis. We first collated independent photo captures of tigers. A relative abundance index (RAI) for tigers was computed for each camera trap station as the sum of total independent tiger photo captures divided by camera trap effort (time that a camera was operational); this is expressed as photo captures per 100 trap nights. Camera traps were then categorised into four RAI categories for tigers following the same classification based on quartiles. At each camera trap station where both tigers and leopards were photo-captured, we calculated the time difference between the detection of tigers (hereafter reference detection) and the closest detection (hereafter proximal detection) of leopards following the initial photo capture of tigers. This time difference between the reference and proximal detections is hereby termed as "minimum lag". We assessed the temporal spacing between consecutive detections of tigers and leopards across high, medium, and low tiger RAI categories.

It was likely that leopards could potentially avoid tigers at the fine spatial–temporal scale. To evaluate such a pattern, we checked the lag in a trail usage by leopards following a photo capture of a tiger. We compared the actual time lag of leopard photo capture following a tiger capture with a random time lag using a Mann–Whitney U test (Mann and Whitney, 1947). We also analysed this pattern in leopard trail usage at (1) low (1.92 tigers per 100 km^2), (2) medium (4.48 tigers per 100 km^2), and (3) high tiger density (4.8 tigers per 100 km^2) categories. These classes were decided based on the three quartiles of tiger density. All analyses were carried out using Microsoft Excel (v. 2007) and the programme R (v. 3.1.3).

3 Results

3.1 Density and distribution pattern

The total effort of 28 742 trap nights over (Table A1) the entire sampling period yielded photographs of 6459 usable photographs of tigers and 1884 usable photographs of leopards. Photographs were of 28 unique male tigers, 27 unique female tigers, 21 unique male leopards, and 30 unique female leopards (individuals over the years) (Table A2). Densities of these sympatric predators were estimated for each sampling year. Estimated tiger density ranged from 4.8 (SE 0.799) to 5.7 (SE 0.879) per 100 km^2 during the study period with overlapping confidence intervals (Table 1). Estimates of density of leopards varied from 3.76 (SE 0.918) to 4.9 (SE 0.884) per 100 km^2. Our data displayed variation in detection probability and sigma according to gender. Detection probabilities of female tigers were higher than males, whereas both male and female leopards showed similar probability of detection for the first 2 years (Table 1). We found similar estimates of sigma for female tigers and leopards and for male tigers and leopards (Table 1).

The average distance between home range centres of tigers and leopards was 13.63 ± 7.03 km with a range of 0.2 to 35 km. The detection corrected sex ratio (*pmix*) of tigers were slightly female-biased in the first 2 years but became male-biased during the last year. On the other hand, leopards were male-biased in the first year, which later became dominated by females in the following years (Table 2). Our data indicate that tigers and leopards were spatially segregated. Tiger captures were higher in the central, south-west, and northern parts of the study area (Fig. 2). Leopard captures were higher in areas of relatively lower tiger densities and peripheral areas where tigers occur less (Fig. 2). Density contours of leopards against that of tigers showed that density of leopards declines with increase in the density of tigers (Fig. 3).

Our results did not show any significant relationship between the distribution pattern of the major prey species (chital, sambar, and wild pigs) with that of tigers and leopards in the study area (Fig. B1). Vegetation cover (NDVI) also showed no relationship (Fig. B2). The slope of the regression for leopard density versus the lower quantile of tiger density was significantly positive; at median density of tigers, it was not different from zero, while at higher tiger density, quantiles were significantly negative (Table 2) (Fig. B3), implying leopard density was lower in high tiger density areas.

3.2 Activity peaks and temporal overlap

Tigers and leopards both had bimodal activity patterns with activity peaks around 06:00 IST in the morning and 19:00 to 20:00 IST in the evening. The extent of temporal overlap between these two sympatric felids was 89 % (CI 86 %–93 %) in 2016 (Fig. 4). In low tiger density areas, the extent of overlap was slightly lower, 77 % (CI 68 %–85 %) (Fig. B4a),

Table 1. Estimated density per 100 km^2 along with sex-specific detection probability ($g0$), sex-specific spatial scale of detection (σ, in km), and detection corrected sex ratio (male : female) of tigers and leopards in Pench Tiger Reserve, Madhya Pradesh, during the study period (2013–2016).

| Session	Species	Model parameters	Density (SE) per 100 km^2	$g0$ (SE) (female)	$g0$ (SE) (male)	Sigma (σ) (SE) (female)	Sigma (σ) (SE) (male)	Sex ratio (M : F) (SE)
2013–2014		$g0[h2]s[h2]$	5.735 (0.879)	0.037 (0.004)	0.025 (0.003)	2.237 (0.108)	3.989 (0.224)	0.956 (0.078)
2014–2015	Tiger	$g0[h2]s[h2]$	4.854 (0.799)	0.053 (0.005)	0.026 (0.003)	2.063 (0.099)	4.404 (0.235)	0.9 (0.081)
2015–2016		$g0[h2]$	5.155 (0.824)	0.068 (0.005)	0.039 (0.003)	2.714 (0.068)	2.714 (0.068)	1.091 (0.082)
2013–2014		$s[h2]$	3.758 (0.918)	0.004 (0.001)	0.004 (0.001)	2.697 (0.435)	4.129 (0.592)	1.194 (0.123)
2014–2015	Leopard	$g0[h2]s[h2]$	4.446 (0.848)	0.026 (0.004)	0.025 (0.006)	1.912(0.158)	3.918 (0.29)	0.495 (0.092)
2015–2016		$g0[h2]s[h2]$	4.97 (0.884)	0.017 (0.003)	0.042 (0.005)	2.402 (0.209)	3.133 (0.236)	0.647 (0.086)
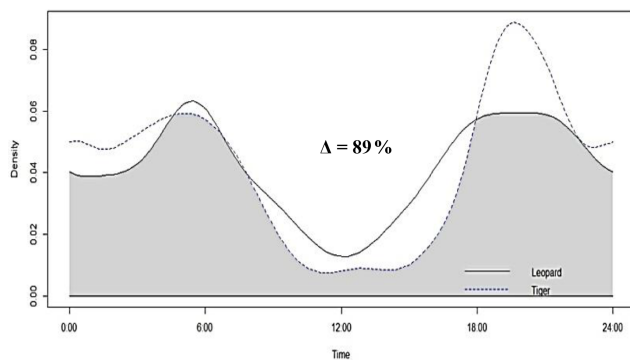
Figure 4. Activity peaks and temporal overlap between tigers and leopards in Pench Tiger Reserve, Madhya Pradesh.

Table 2. Quantile regression coefficients of leopard densities with tiger densities in Pench Tiger Reserve, Madhya Pradesh, during 2013–2016.

Quantiles	Coefficient (± 95 % CI)	p values
0.25	0.393 (0.118–0.562)	0.0001*
0.5	0.13 (0.048–0.191)	0.148
0.75	−0.072 (−0.162−−0.037)	0.348
0.95	−0.37 (−0.434−−0.074)	0.000001*

but with overlapping confidence intervals. In medium and high tiger density areas, the extent of temporal overlap was similar, 86 % (CI 85 %–99 %) and 86 % (CI 81 %–93 %), respectively (Fig. B4b–c). The coefficients of temporal overlap were also similar across years with overlapping confidence intervals, 77 % (CI 69 %–86 %) in 2014 and 88 % (CI 79 %–92 %) (Fig. B5a–b). Investigation of the extent of temporal overlap between these two sympatric felids and their principal prey revealed that the maximum overlap for both tigers and leopards was with sambar, followed by wild pigs and then chitals (Fig. B6a–f).
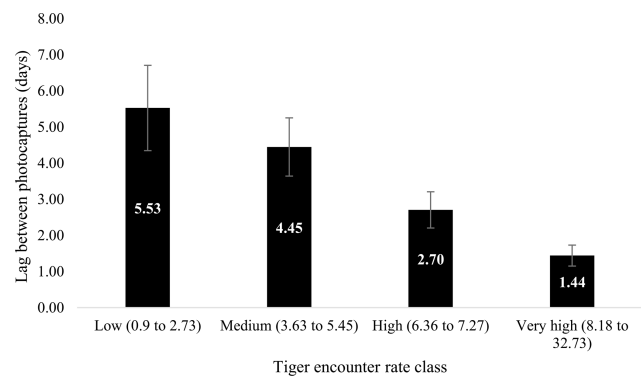
Figure 5. Relationship between average minimum lag between photo capture of a leopard after a tiger has been photographed. Columns represent the average encounter rate of tigers (classified low as lower quantile or least encounter rate and very high as upper quantile or maximum encounter rate of tiger).

3.3 Temporal spacing of detections at shared camera sites

Minimum lag between successive captures of tigers and leopards ranged from 0.002 to 36.29 d (Fig. 5). Lowest average minimum lag was seen in very high tiger encounter rate class (1.311 ± 0.87 d), whereas the highest lag was in low tiger encounter rate class (6.84 ± 1.84 d). Mean lag varied from 1.88 (SE 0.63) d to 12.61 (SE 1.95) d (Fig. 5). Our data showed that the mean lag and average minimum lag decreased with increase in the tiger encounter rate in a linear manner (Fig. 5). In the high encounter rate class, the minimum lag varied from 0.002 to 8.65 d, whereas the range of minimum lag was 0.02 to 19.96 and 0.03 to 36.29 d in medium and low encounter rate class, respectively.

The median time lag between leopard captures after a tiger capture was 1.68 d, whereas the median time lag between tiger capture and a random capture event was 3.63 d, and the observed lag was significantly smaller than random ($W = 11\,617$, $p = 0.00005$). We also found that the observed lag was significantly smaller than random lag in medium

($W = 1617$, $p = 0.0003$) and high ($W = 1288$, $p = 0.03$) tiger density areas. However, the observed lag was not different than random in the low tiger density areas ($W = 1001$, $p = 0.29$).

4 Discussion

The interactions among the members of the predator guild significantly influence their population dynamics and distribution (Linnell and Strand, 2000). Understanding the patterns of interactions provides insights into mechanisms that promote coexistence between competing carnivores. Our study adds information on how tigers and leopards co-occur at high densities through fine-scale spatio-temporal interactions.

4.1 Tiger and leopard density pattern

Tiger density in the study area was on par with estimates from reserves with similar habitat features like Bandhavgarh Tiger Reserve and Pench Tiger Reserve, Maharashtra (Jhala et al., 2020). Estimated leopard density during the study period was similar to that of Bandhavgarh Tiger Reserve (Rather et al., 2021). The densities of these two sympatric predators within the study area remained stable (overlapping confidence intervals) throughout the 3 years. Estimation of prey density-based carrying capacity (Jhala et al., 2020) shows that the carrying capacity of the study area varies between 6.96 to 8.86 tigers per $100\,km^2$. Carrying capacity of leopards based on prey biomass (Hayward et al., 2007) was estimated at 8.07 leopards per $100\,km^2$. As per our findings and the latest estimates of tiger and leopard densities in the area (Jhala et al., 2020), it can be assumed that tigers are about to attain carrying capacity in PTR, MP. Comparison with the estimated leopard carrying capacity suggests that leopards are operating below the carrying capacity. We did not observe any evidence of decline in leopard population over the years. Such lack of demographic effect on leopard population in the presence of tigers has also been observed in Kanha National Park where leopards attain a positive growth rate in areas of low and medium tiger density (Kumar et al., 2019).

As per our hypothesis, leopard densities decreased with increase in tiger density at higher quantiles. The areas of low tiger density were also comparatively low in prey abundance. As a result, both these co-predators can increase their numbers to a certain extent by exploiting these limited resources. At medium tiger densities, no relationship was seen between tigers and leopards, and at high tiger densities, a depressive effect of tiger density was observed on leopard densities.

4.2 Spatial distribution pattern of tigers and leopards

We also found that photographic captures of leopards were higher near the periphery (except the northern and south-western part) and areas of PTR where photo captures of tigers were lower (Fig. 2). PTR is situated in a matrix of agricultural fields and human habitation. The northern and south-western part of PTR is connected with the reserve forest, which has abundant prey and resulted in higher photo captures of tigers, whereas the rest of the periphery where leopard captures were higher borders agricultural fields and/or human habitation. Similar findings are reported from Bardia National Park, Nepal, and Rajaji National Park, India, where leopards use the edges as a result of interference interactions with tigers (Odden et al., 2010; Harihar et al., 2011). The relative avoidance of peripheral (except for the south-west and northern part) areas by tigers probably created a "competition refuge" (Odden et al., 2010) for leopards near the periphery of PTR. Different species with similar prey preferences residing in the same area are likely to avoid vigorous interactions owing to the huge cost associated (Donadio and Buskirk, 2006; Ramesh et al., 2012; Vanak et al., 2013; Carter et al., 2015). However, intraguild killing of the subdominant predator by the dominant one can take place even in the absence of strong competitive dynamics (Curveira-Santos et al., 2021), but we did not observe tiger predation on leopards during the study period.

Competition acts as a major driving force in structuring communities in ecosystems with multiple predators because of their behavioural and morphological adaptations to hunt successfully (Creel, 2001; Donadio and Buskirk, 2006; Balme et al., 2017). Majumder et al. (2012a) reported significant dietary overlap between tigers and leopards in PTR, but leopards were seen to be feeding largely on prey with poorer health condition (Majumder et al., 2013). Resource partitioning has been well documented as a mechanism for the coexistence of sympatric predators (Sollmann et al., 2012; Santos et al., 2019; Paúl et al., 2020). Our study supports the fact that leopards are adaptive in terms of choice in the presence of tigers. The risk of exploitative competition for leopards with tigers is higher, as shared prey leads to enhanced competitive interactions.

4.3 Temporal activity pattern of tigers and leopards

In addition to spatial and prey partitioning, temporal partitioning has also been observed as an adapted behavioural mechanism of these sympatric predators to attain coexistence (Steinmetz et al., 2013; Sunarto et al., 2015; Yang et al., 2018). The conventional analysis of unitary encounter rate and temporal activity peaks (Fig. 4) of our data does not show any sign of difference. Temporal overlap between these two sympatric predators also remained similar across varying tiger density areas. Both these predators need not separate in daily activity patterns, as it overlaps with the daily activity pattern of their principal prey species (Fig. B1a–f). High temporal overlap between sympatric predators in order to maximise their utilisation of prey has been observed in previous studies (Karanth and Sunquist, 1995; Ramesh et

al., 2012). Hayward and Slotow (2009) also mention that despite all members of the guild facing the risk of intraguild predation, only secondary predators like wild dogs and cheetahs alter their activity pattern to minimise overlap with major kleptoparasites like lions and leopards, whereas the latter do not show any such pattern. Predators opt for strategies that allow them to maximise their nutrient intake given the constraints of resources like prey density and habitat. It can vary widely for the same species at different parts of their geographical distribution (Sunquist and Sunquist, 1989). Leopards in PTR, which are majorly restricted to suboptimal areas, do not exhibit temporal avoidance of tigers in order to ensure their survival by optimising their hunting opportunities.

4.4   Co-occurrence patterns of tigers and leopards

Both tigers and leopards were captured in 79 % of all the camera stations, but their rate of captures varied significantly. However, in our study, we found no evidence of leopards avoiding tigers at fine spatial–temporal scale, as we did not find any difference between trail usage by leopards following a tiger photo capture and a random trail usage. This pattern was the same at different tiger densities. Homogeneous distribution of the preferred prey species and greater visibility of the study area (Karanth et al., 2017) might be responsible for the absence of such fine-scale behavioural avoidance mechanisms.

We used only camera trap-based data for this study, so any reactive avoidance (Broekhuis et al., 2013) of leopards towards tigers could not be observed. We did not encounter any evidence of intraguild predation or kleptoparasitism during the entire study period, as our study was primarily based on camera traps and ad libitum observations. Behavioural observations of these animals with the help of radiotelemetry where they coexist in high densities can further elucidate their avoidance mechanisms. Additionally, it can generate insights into kill rates and prey handling of these two predators, which are essential in understanding their dietary niche composition and interference interactions (Miller et al., 2014; Elbroch et al., 2014). Such studies have the scope of investigating the process of interspecific social dominance and coexistence of sympatric predators effectively.

5   Conclusions

Leopards co-occur with tigers in majority of the places in Asia and they have the most widespread distribution among all the felids (Nowell and Jackson, 1996; Henschel et al., 2008; Odden et al., 2010). Their extent of spatial overlap with intraguild predators is also the highest along with extreme vulnerability to exploitative competition (Caro and Stoner, 2003; Du Preez et al., 2017). Intraguild competition has the ability to push the subordinate predators in suboptimal habitats, which can impact their survival. However, leopards have

been known to use these suboptimal habitats to their maximum extent, which are not preferred by tigers and are areas near human presence (Odden et al., 2010; Athreya et al., 2013), whereas tigers usually need relatively larger undisturbed areas with ample wild prey for their survival (Karanth and Stith, 1999).

Our study provides a record of tiger–leopard co-occurrence patterns over multiple years and generates insights into the behavioural and ecological mechanisms adapted by these two predators. Our findings substantiate the fact that dominant predators can influence the spatial distribution pattern of the subordinate predators, but abundance response depends on habitat features (Ritchie and Johnson, 2009; Broekhuis et al., 2013; Vanak et al., 2013; Swanson et al., 2016; Balme et al., 2017). Our results suggest that areas with a high density of tigers were detrimental for leopard density, and it seems likely that they depress or prevent occupancy of other large carnivores as well (dholes, sloth bears, and wolves) (Steinmetz et al., 2013; Rayan and Linkie, 2016, Lahkar et al., 2021). Our results along with a study of dietary habits of tigers and leopards in PTR (Majumder et al., 2012a) indicate that partitioning of either spatial or dietary niche can aid in two large predators to co-occur, but prey and habitat characteristics also play a crucial role in determining the results of intraguild interactions (Janssen et al., 2007; Harihar et al., 2011; Balme et al., 2017). However, we did not find any evidence of temporal segregation or fine-scale spatio-temporal avoidance between these two sympatric predators.

Our study provides a record of ecological and behavioural adaptations in a natural system to attain co-occurrence. This increases the ecological understanding of these species and provides basis for scientific management programmes. As targeted management practices for one flagship species can negatively affect the subdominant predators (Karanth et al., 2011; Harihar et al., 2011; Lahkar et al., 2021), understanding intraguild interactions of these two sympatric predators is essential. The zeal of increasing tiger abundance can have detrimental impacts on the carnivore community. However, it may be relevant to state that many of the other large carnivores are also found at reasonable densities outside of the PAs (Jhala et al., 2020, 2021). While source populations of tigers are primarily restricted to within PAs even though 40 % of the tiger population of India resides outside of tiger reserves, these are essentially low-density tiger areas which serve as sink habitats. Thus, tigers are a conservation-dependent species and need legal protection.

Appendix A
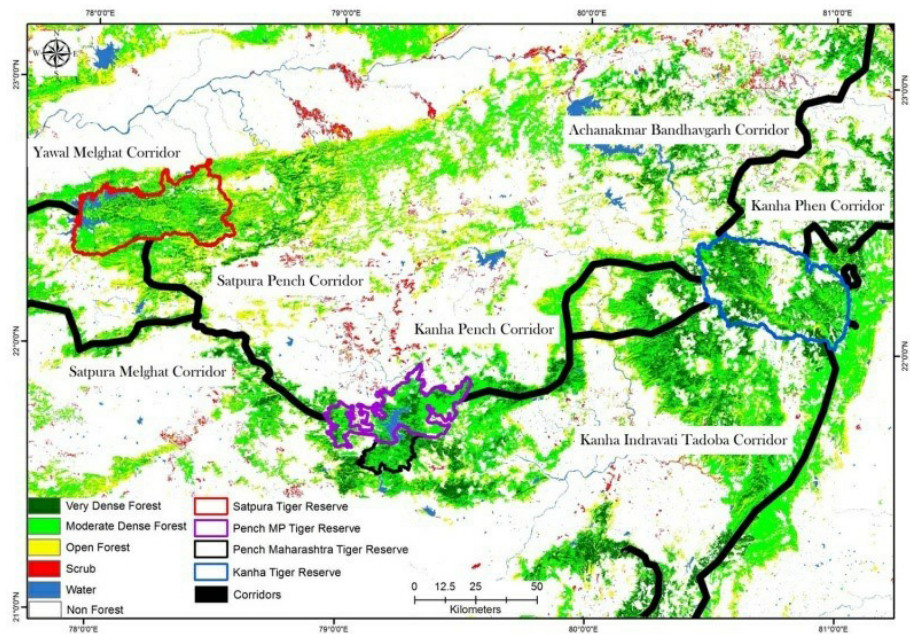
Figure A1. Location of Pench Tiger Reserve, Madhya Pradesh, in the central Indian tiger landscape along with its corridors with the surrounding protected areas (PAs). This map is reproduced from a study on connecting tiger populations for long-term conservation (Qureshi et al., 2014).

Table A1. Camera trapping efforts in Pench Tiger Reserve, Madhya Pradesh, during 2013–2016, (* MCP: minimum convex polygon).

Session	Total number of camera traps	MCP^{3*} (km^2)	Total trap nights	Number of identifiable photographs	
				Tiger	Leopard
2013–2014	82	410	9072	1656	511
2014–2015	84	410	10 080	2109	689
2015–2016	82	410	9320	2694	684

Table A2. Details of camera trap-based photographs of individually identified tigers and leopards over the entire study period (2013–2016). The bold highlighted portion includes photo capture details of cubs of tigers and leopards, respectively, which were not included for analysis. NA stands for not applicable.

Session	Species	Age class	Male	Female	Cubs	Unidentified Gender	Total
2013–2014	Tiger	Adult	16	25	NA	3	44
2014–2015			18	20	NA	0	38
2015–2016			21	18	NA	1	40
2013–2014		Cubs	NA	NA	1	0	1
2014–2015			NA	NA	7	0	7
2015–2016			NA	NA	25	0	25
2013–2014	Leopard	Adult	9	12	NA	4	25
2014–2015			17	20	NA	4	41
2015–2016			25	15	NA	2	42
2013–2014		**Cubs**	**NA**	**NA**	**1**	**0**	**1**
2014–2015			NA	NA	3	0	3
2015–2016			NA	NA	3	0	3

Appendix B

(a)   (b)
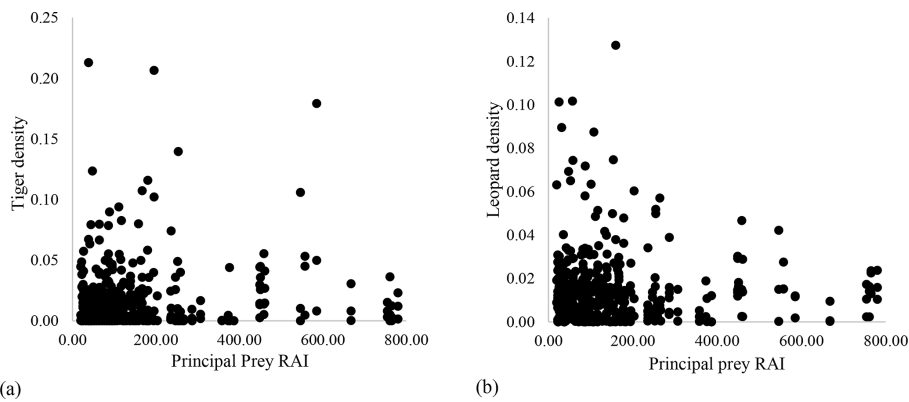
Figure B1. Relationship between prey relative abundance index (RAI) and **(a)** tiger density and **(b)** leopard density in Pench Tiger Reserve, Madhya Pradesh.

(a)   (b)
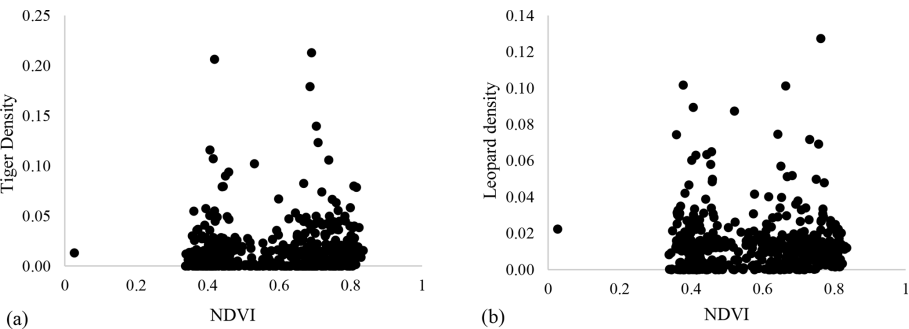
Figure B2. Relationship between vegetation cover (NDVI) and **(a)** tiger density and **(b)** leopard density in Pench Tiger Reserve, Madhya Pradesh.
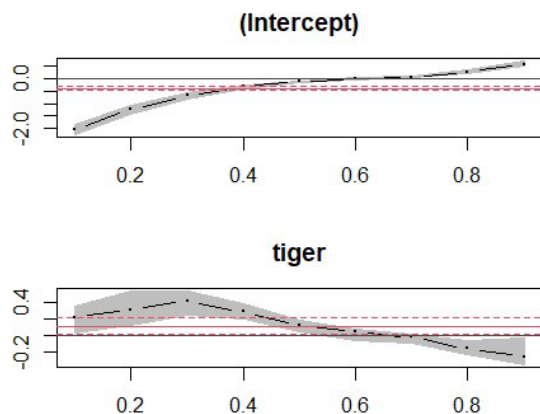
Figure B3. Slopes of quantile regression of effects on tiger density on leopard density where leopard density declines in higher quantiles.
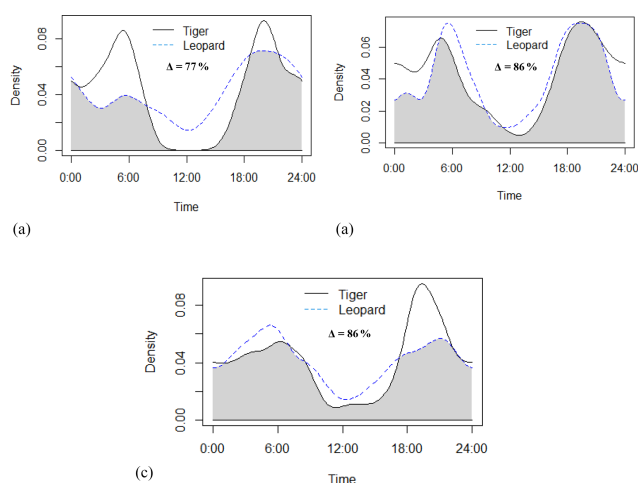
Figure B4. Activity curves and extent of temporal overlap between tiger and leopard in **(a)** low tiger density, **(b)** medium tiger density, and **(c)** high tiger density areas in Pench Tiger Reserve, Madhya Pradesh.

Figure B6. Activity curves and extent of temporal overlap between **(a)** tiger and sambar, **(b)** tiger and wild pig, **(c)** tiger and chital, **(d)** leopard and sambar, **(e)** leopard and wild pig, and **(f)** leopard and chital in Pench Tiger Reserve, Madhya Pradesh.
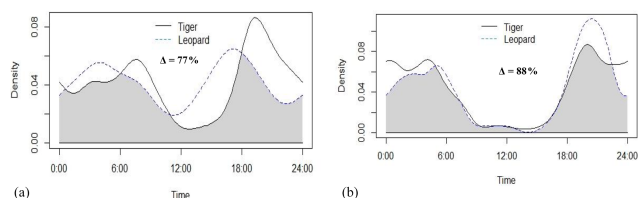
Figure B5. Activity curves and extent of temporal overlap between tiger and leopard in **(a)** 2014 and **(b)** 2015 in Pench Tiger Reserve, Madhya Pradesh.

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