Spatial and Temporal Responses of Leopard (*Panthera pardus*) in the Presence of Tiger (*Panthera tigris tigris*) in Rajaji National Park, Uttarakhand

Thesis submitted for the award of the Degree of
Masters *in* **Wildlife Science**

by

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to

Saurashtra University

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DECLARATION

I, **Anubhuti Krishna**, hereby declare that the research work entitled "**Spatial and Temporal Responses of Leopard (*Panthera pardus*) in the Presence of Tiger (*Panthera tigris tigris*) in Rajaji National Park, Uttarakhand**", carried out in partial fulfilment of M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot is original research. This research work was carried out under the supervision of Dr. Salvador Lyngdoh and Dr. Samrat Mondol, at the Wildlife Institute of India from January 2021 to July 2021. I hereby declare that this work has not been submitted for any other degree of any university.

Anubhuti.

Date: 13th August, 2021
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CERTIFICATE

This is to certify that Ms. Anubhuti Krishna has carried out original research titled "**Spatial and Temporal Responses of Leopard (*Panthera pardus*) in the Presence of Tiger (*Panthera tigris tigris*) in Rajaji National Park, Uttarakhand**" in partial fulfilment of Master's Degree in Wildlife Science from Saurashtra University, Rajkot. This study was carried out under our supervision from January 2021 - July 2021. We hereby certify that this work has not been submitted for any other degree to any other university.

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LIST OF ABBREVIATIONS

- RNP – Rajaji National Park
- RTR – Rajaji Tiger Reserve
- WR – Western Rajaji
- ER – Eastern Rajaji
- RAI – Relative Abundance Index
- CI – Confidence Interval

EXECUTIVE SUMMARY

Leopards co-occur with tigers in several parts of Asia as well as over a major portion of their geographical distribution in India. A clear dominance hierarchy establishes between the two felid species in regions of sympatry with tigers, owing to stark body size differences, holding higher ground. The striped felid, thus, invokes numerical as well as functional responses in their less dominant counterparts. The current study aims at understanding the spatial and temporal patterns of leopards in the presence of tigers. Rajaji National Park in Uttarakhand offers an excellent natural setup for understanding such intra-guild interactions as the western part of the Park hosts leopards but is devoid of tigers and the eastern region has sympatric populations of the two felid species. These act as control and experimental setups respectively, and hence this site was chosen for conducting the field sampling. It was found that leopards exhibit some degree of spatial segregation from tigers as was evidenced by differences in the activity hotspots of the two felids in Eastern Rajaji. This is attributable, at least in part, to tigers as a negative relationship was obtained between space use by tigers and leopard occupancy under the occupancy framework. Temporal patterns, on the other hand, revealed a rather interesting trend. The diel activity of leopards in Eastern Rajaji, i.e., in the presence of tigers was very different from that of leopards in the western part of the Park. The activity of the latter was distributed throughout the day with nocturnal peaks of low intensity. The former, however, showed an activity pattern restricted to the nocturnal hours with very little activity during the day. The temporal peaks for this population also showed greater intensity than that of the pattern observed in the western leopard population. These peaks of activity, however, contrary to expectations, coincided with those of tigers in the landscape. Since predator-prey interactions also play an important role in shaping the temporal activity patterns of carnivores, the temporal overlaps between the two felids and their potential prey was also analysed. This too failed to offer an explanation to the rather

unexpected leopard diel pattern in ER. It was subsequently observed that though leopards might have similar temporal activity to that of tigers, they are rarely at the same place at the same time. A clear lag was observed between leopard captures at camera traps following photo-captures of tigers at the same location. Hence, a combination of spatial and temporal segregation might be at play at a finer scale than at the population level and requires further examination in order to elucidate the interactions and mechanisms of sympatry between leopards and tigers in this landscape.

1. INTRODUCTION

Leopards are the most widely distributed of all wild cat species (Bailey 1994; Jackson and Nowell 1996). They are majorly solitary and highly adaptable, and are found across a broad variety of habitats (Bailey 1994; Daniel 2009). Globally, they are known to occur from across Africa to South Asia, northwards to Central Asia and all the way to the Amur valley in Russia in the east (Bailey 1994). Within the extent of the country, leopards are found occupying areas more or less throughout with the exception of desert areas and the mangrove areas of the Sunderbans (Khan and Beg 1986). Despite the vast expanse of land this species occupies, it falls under the ‘Near Threatened’ category of the IUCN Red List. It enjoys the highest levels of legal protection as it is not only included in Schedule I of the Indian Wildlife (Protection) Act 1972 but also listed in Appendix I of CITES.

Across several parts of Asia as well as in India, these cats are known to occur sympatrically with their larger striped counterparts, tigers (Seidensticker 1976). These top predators demonstrate cascading effects on herbivores directly and on plants by extension, thus playing a pivotal role in regulating ecosystems (Terborg et al. 1999). In addition to this top-down effect along linear food chains and simple food webs, it was subsequently understood that top carnivores also exerted their controlling effect on other species within the same guild such as mesocarnivores (Morrison et al. 2007; Ritchie and Johnson 2009; Ripple et al. 2014).

Between tiger and leopard, the former most certainly dominates the latter due to sheer difference in body size (Karanth and Sunquist 1995). This renders the two unequal competitors and there is establishment of a clear dominance hierarchy between them. Competition, and by extension dominance, is especially stiff as the two species closely resemble ecologically. Foundations for this phenomenon can be recognised as early as 1934, with Gause’s competitive exclusion principle stating that species occupying the same niche cannot coexist in the same environment. The more dominant species would ultimately exclude the less dominant one. The interactions between the dominant species, tiger and their sub-dominant counterpart, leopard can range from benign to fatal. High densities of the apex predator lead to increased encounter rates between the two species. Under such circumstances, the sub-ordinate carnivore may be compelled to avoid using sites used by the dominant predator (Ramesh et al. 2012). Stated otherwise, there is active avoidance of the dominant carnivore by its less dominant counterpart and this can lead to shifts in habitat usage of the latter (S. Lima and Dill 1990). Such interactions, however, may have more radical outcomes than avoidance. For instance, several accounts of inter-specific killing, also known as intra-guild predation have been recorded over the years (Polis and Holt 1992).

Intra-guild dominance often manifests as a numerical response embodied by the reduction in densities, growth and fecundity of the sub-dominant species as well as its altered age structure at the level of the population (MacNally 1983; Petren and Case 1998). This holds true for tiger – leopard systems as well and is demonstrated by previous studies conducted in Sariska (K. Mondal et al. 2012) and Rajaji (Harihar, Pandav, and Goyal 2009), where an increase in the tiger population was coupled with a decline in the population of leopards.

Species interactions, however, in addition to numerical changes, also elicit behavioural responses. Such responses can be along different niche axes and can affect sympatric associations as well as predator-prey relationships, and can consequently mediate co-existence of competing sympatric carnivores. Major niche axes along which such shifts are observed include dietary, spatial and temporal components.

Segregation in terms of diet has been shown to be a strong driver for coexistence of large carnivores in previous studies conducted in Nagarhole National Park (Karanth and

Sunquist 1995) as well as Bandipur Tiger Reserve (Andheria, Karanth, and Kumar 2007). However, coexistence of morphologically and ecologically alike species and avoidance of inter-specific competition is also possible through behavioural mechanisms resulting in spatial and/or temporal segregation (Pianka 1974; Schoener 1974; Durant 1998). An excellent example of spatial segregation comes from the study conducted in Sariska Tiger Reserve post tiger reintroduction, which clearly showed separation between tigers and leopards along the spatial niche axis (K. Mondal et al. 2012). Often the sub-dominant species may occupy sub-optimal areas in order to avoid individuals of the dominant species (Chesson 1986; Rosenzweig 1991; Durant 1998). An evident pattern of temporal segregation was also observed in the aforementioned system. Thus, intra-guild competition can be reduced if ecologically and morphologically similar species partition their temporal niche (Bitetti et al. 2009; Kronfeld-Schor and Dayan 2003). This helps mediate aggregation risk and competition for resources. It has also been observed that even in systems with large sympatric carnivores showing high temporal overlaps, segregation tends to occur at least during their respective peaks of activity (Dias et al. 2019; Penido et al. 2017).

However, being hypercarnivores, prey driven responses also play an important role in determining spatio-temporal patterns of leopards in addition to competition and dominance driven responses. Activity of predators has previously been shown to be positively correlated with that of their prey (Luttbeg and Sih 2004). Diel activity of many felids is also associated with the activity patterns of their respective prey species (Harmsen et al. 2011). Therefore, while prey species avoid time of high predator activity, predators align their activity patterns according to that of the prey (Berger and Gese 2007; S. L. Lima and Bednekoff 1999) leading to a constant ‘arms race’ between the hunter and the hunted.

Hence, there exists a delicate balance between avoiding competition (dominant competitor avoidance hypothesis) and seeking prey (prey synchrony hypothesis). As a result, sub-dominant predators such as leopards neatly nestle between the dominant predator and prey strata in the ecosystem.

It is due to this control exerted by the apex predator that the sub-dominant counterpart remains in check. However, just as much as dominant predators exert pressure, their removal or eradication from the system may lead to an explosion in the population of the sub-dominant predator. This is a process commonly known as mesopredator release. At this stage, it becomes important to define what exactly entails a mesopredator. Over the years, several varying explanations for what counts as a mesopredator have emerged. However, for the term to be rooted in ecological theory, a mesopredator should be defined as any midranking predator in a food web, regardless of its size or taxonomy. Hence, a mesopredator in one ecosystem may be an apex predator in another, and one ecosystem may have multiple mesopredators (Roemer, Gompper, and Van Valkenburgh 2009). A mesopredator is therefore best identified based on the characteristics of a given food web rather than characteristics of the individual species (Prugh et al. 2009). Then, by extension, mesopredator release can be defined as collapses in top predator populations associated with a dramatic increase in the abundance of a smaller carnivore (Prugh et al. 2009). As increasingly higher population losses are seen for apex predators, the phenomenon of mesopredator release is expected to become more prevalent. When an apex predator is fully eradicated in an ecosystem, the mesopredator directly below the former apex predator in the trophic hierarchy may serve as a replacement (Prugh et al. 2009). This is termed as ascendancy of a mesopredator and is also likely the case with leopards in Western Rajaji post the eradication of tigers from the landscape.

The top down processes of a large carnivore guild are not yet fully understood (Finke and Denno 2005) and the knowledge of incomplete guild functioning, that is, effect of removing one of the components of a guild, is also lacking. This assumes greater importance in the context of current global large predator losses (Hayward and Slotow 2009). Hence, the current study aims at examining how a dominant predator such as tiger influences the spatio-temporal patterns of a sub-dominant predator such as leopard.

1.1 Objectives

The specific objectives and research questions of the present study are:

1. To evaluate spatial niche segregation between leopard (*Panthera pardus*) and tiger (*Panthera tigris tigris*) in Eastern Rajaji National Park.
    i. Do leopards segregate from tigers in terms of space use?
2. To evaluate temporal niche selection of leopard (*Panthera pardus*) in the presence and absence of tiger (*Panthera tigris tigris*).
    i. Does the temporal activity pattern of leopards differ from that of tigers in Eastern Rajaji?
    ii. Does the temporal activity pattern of leopards differ in the presence and absence of tigers?

1.1.1 Hypotheses

Leopards and tigers are the apex predators in Rajai National Park. However, there is a clear dominance hierarchy between the two, with tigers holding the upper hand. Hence, in Eastern Rajaji (ER), that is, in the presence of the greater predator, tiger, the sub-dominant predator, leopard may show niche segregation in order to co-exist in the same system. It is, therefore, hypothesised that leopards and tigers will show segregation in terms of space use. It is also expected that they will have differing temporal patterns. Conversely in Western Rajaji (WR), in the case of absence of the dominant predator, the sub-dominant carnivore may display changes only with respect to niche utilisation. It is also suspected that the temporal pattern of leopards in Eastern Rajaji, i.e., in the presence of tigers will be distinct from that in Western Rajaji, i.e., in the absence of the dominant predator.

Therefore, the current study hypothesises that the presence of a dominant predator, i.e., tiger will influence the niche selection of a less dominant predator, leopard. This will manifest itself along the spatial and/or temporal niche axes. Alternatively, in the absence of tiger, leopard activity will be determined by resource availability.

2. STUDY AREA

The Rajaji Tiger Reserve (RTR) is situated in and falls entirely within the Indian state of Uttarakhand. It was named after C. Rajagopalachari, the first Governor General of India. It is constituted by 13 ranges, three of which, namely Shyampur, Laldhang and Kotdwar, comprise the buffer zone of the reserve. The remainder of the 10 ranges form the Rajaji National Park (RNP), the core zone of RTR. The Park was notified and established in the year 1983 as an amalgamation of three previously recognized protected areas – the Rajaji Sanctuary, Motichur Sanctuary and Chilla Range of Pauri Forest Division, and was subsequently declared a tiger reserve by the NTCA in April 2015.

Rajaji National Park extends between 29°15' and 30°31'N latitudes and 77°52' and 78°22'E longitudes covering an area of 820.42 km^2 (Joshi and Dixit 2012). It spreads across three districts of Uttarakhand namely Dehradun, Haridwar and Pauri. The Ganges flowing through the Park in the North-South direction splits it into two regions – Western Rajaji and Eastern Rajaji. The western part is a constituent of tiger habitat block I (THB I) of the Terai Arc Landscape (TAL) whereas the eastern portion falls within tiger habitat block II (THB II) of TAL. Western Rajaji consists of seven ranges namely Ramgarh, Kansrao, Motichur, Chillawali, Dholkhand, Beribara and Haridwar. The former three form the northern part of Western Rajaji while the latter four constitute the southern portion. Eastern Rajaji on the other hand consists of the three ranges of Chilla, Gohari and Rawasan.

Over the years the Park has come to be surrounded on almost all sides by human habitation in the form of settlements ranging from small villages and suburban towns to large cities such as Haridwar and Rishikesh. While Eastern Rajaji remains connected to Corbett Tiger Reserve and further eastward reaches of the TAL, Western Rajaji sits more or less isolated. In addition to the natural barrier offered by the Ganges to the movement of animals, several anthropogenic factors such as construction of linear infrastructure (roads and railways) and dams as well as urbanization has led to the Chilla-Motichur corridor, which previously connected the two parts of the Park, becoming virtually dysfunctional thus leading to little or no dispersal from the eastern portion of the Park to the western side.

2.1 Geology

Rajaji lies at the southern foothills of the Himalayas. It encompasses the Shivaliks and the upper reaches of the vast Indo-Gangetic plains (Rasaily 2012). This region sports a unique geological history. The collision of the Indian plate into the Asian plate gave rise to the Himalayas. This was followed by the descent of several glaciers from the newly formed mountain range. The depositions of these glaciers coupled with further upliftment has given rise to the Shivaliks (Rasaily 2012). The rounded boulders seen in the area, commonly known as rolling stones, are testament to the glacial origin of the region. The soil depth here rarely exceeds a few feet and the surface is highly porous. As a result, flowing surface water is rarely seen in this area. Instead, the movement of water is sub-terranean (Harihar and Pandav 2012). This region, characterised by a low water table, is known as the ‘Bhabhar tract’. As we move towards the Indo-Gangetic plains the water resurfaces and forms perennial water channels. This region is called the ‘Tarai’.

The terrain of the Park is rugged and undulating, and shows variation in elevation ranging from about 250m to 1100m (Joshi and Dixit 2012). The highly dissected hills are characterized by loose soil and boulders, hence forming a fragile erosion prone system. The Shivalik ridge runs linearly from west to east along the middle of the park. As we move towards the northern and southern park boundaries and away from the ridge, the hills give way to flatter terrain. The most striking topographical feature of the region is the dried river beds locally known as ‘*rau*’ (Rawat and Bhat 1995). The rounded rolling stones, characteristic of this landscape, also form the basal substrate of these water channels. The *raus* are water filled during the monsoon and remain dry throughout the rest of the year owing to the sub-terranean flow of water in the area.

2.2 Climate

Winter, summer and monsoon are the three seasons of the year. The winter typically extends from the month of November to February and is characterized by low temperatures coupled with low humidity. Day temperatures range from about 12-25°C. As the month of March arrives, the cold gives way to warmer weather with the advent of summer. Temperatures peak around the month of June and can reach as high as 38-40°C. The summer months remain mostly dry apart from a few thunderstorms and thus provide perfect conditions for the occasional forest fire. Rainfall increases after the month of June and marks the beginning of the monsoon season characterized by increased humidity. The mean annual precipitation in the area is about 1200-1500mm.

2.3 Vegetation

The overall vegetation of the area is of the subtropical moist deciduous type. It can be further divided into six major subtypes – sal forest, mixed forest, riverine forest, scrubland, grassland and subtropical pine forests (Rasaily 2012). Some of the major influencing factors resulting in these varied vegetation types include aspect, topography and past management practices. The vegetation of the north-facing slopes is markedly different from that of the south-facing ones. This can be attributed to differential rainfall and intensity of sunlight along the two. This compounded with the differential retention of moisture due to the existing vegetation gives rise to wetter *Shorea robusta* (sal) forests on the northern slopes as opposed to drier majorly mixed forests along the southern slopes. Common tree species constituting these mixed forests include *Aegle marmelos*, *Anogeissus latifolia*, *Holoptelia integrifolia*, *Lagerstroemia parviflora*, *Ehretia laevis* and *Terminalia tomentosa* among others. Topography also plays an important role in shaping the vegetation structure. Regions of high elevation are characterized by pine forests and steep cliffs by *Eulaliopsis binata* (bhabar grass). These give way to grasslands in the plain regions of the park. The undisturbed valleys support vast stretches of *Saccharum spp*. whereas short grasslands of *Chrysopogon fulvus, Imperata cylindrica* and *Eragrostis spp.* are found in intensively grazed regions. Plantations of *Tectona grandis* (teak) and *Ailanthus excelsa* can also be found in some areas of the park as residuals of past management practices.

2.4 Fauna

The Park boasts of a diverse assemblage of fauna including mammals. Only a single species of large felid, that is, leopard *Panthera pardus*, is majorly found in Western Rajaji. The population of tigers *Panthera tigris tigris* is limited to only three individuals in this region of the park. Eastern Rajaji on the other hand supports the sympatric occurrence of both tigers and leopards. Other large bodied carnivores and omnivores such as striped hyena *Hyaena hyaena*, Asiatic black bear *Ursus thibetanus* and sloth bear *Melursus ursinus* are also found in good numbers in the eastern region of the park with only few occasional sightings or photographic captures in Western Rajaji. The megaherbivore, the Asiatic elephant *Elephas maximus* is found throughout RNP. Some species of smaller carnivores and omnivores found across both Western and Eastern Rajaji include jungle cat *Felis chaus*, rusty spotted cat *Prionailurus rubiginosus*, leopard cat *Prionailurus bengalensis*, golden jackal *Canis aureus*, Indian fox *Vulpes bengalensis*, common palm civet *Paradoxurus hemaphroditus*, small Indian civet *Viverricula indica* and grey mongoose *Herpestes edwardsii*. Major species of wild prey found in RNP are barking deer *Muntiacus muntjak,* chital *Axis axis*, sambar *Rusa unicolor*, wild pig *Sus scrofa*, goral *Nemorhaedus goral,* nilgai *Boselaphus tragocamelus* (western region only), langur *Semnopithecus hector*, Rhesus macaque *Macaca mulatta*, Indian peafowl *Pavo cristatus*, red junglefowl *Gallus gallus*, Kalij pheasant *Lophura leucomelanos*, porcupine *Hystrix indica* and black naped hare *Lepus nigricollis* (Krishnendu Mondal et al. 2011; Karanth and Sunquist 1995). Domestic prey species include cattle, and feral dogs and cats which are majorly found near the park boundary or might be individuals that have accidentally strayed into the park.

The current study was conducted in the ranges of Haridwar, Beribara and eastern parts of Dholkhand in Western Rajaji. These regions harbour only leopards and act as a control, thus helping establish a baseline for the study. In Eastern Rajaji, the ranges of Chilla and Rawasan were sampled. These are regions of sympatric occurrence of tigers and leopards and thus act as the experimental setup to understand the spatio-temporal patterns of leopards in the presence of a more dominant predator, that is, tiger.

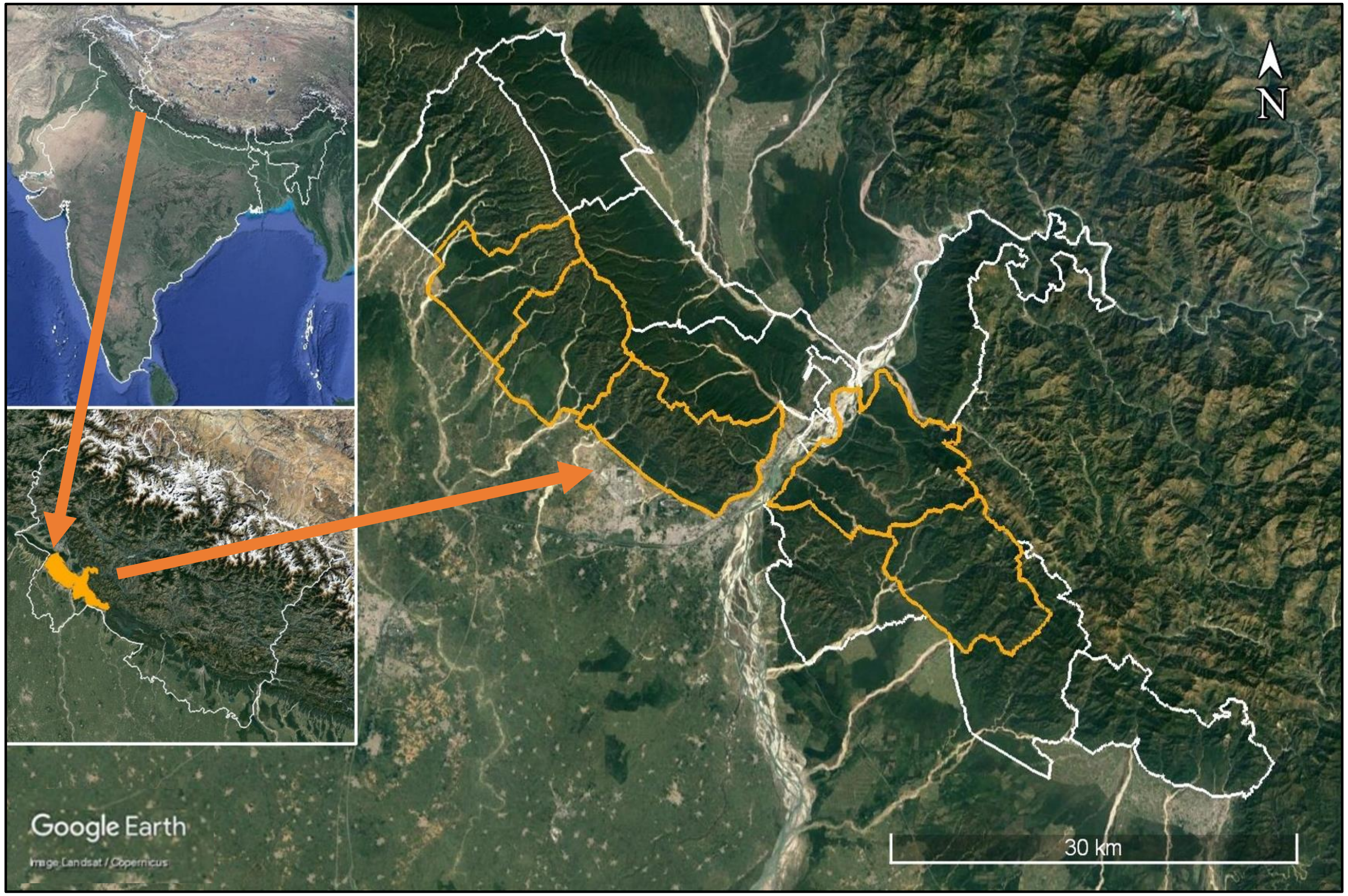

Figure 1. Map showing the ranges of Rajaji Tiger Reserve with insets elucidating the location of the protected area. The ranges sampled for the current study are highlighted in orange. From left to right these are Dholkhand, Beribara, Haridwar, Chilla and Rawasan

3. METHODOLOGY

3.1 Field Methods

The current study is aimed at understanding the influence of a more dominant predator, that is, tiger on the spatio-temporal patterns of leopards in Rajaji National Park. To achieve this, information on space and temporal usage by leopards along with their co-predators and prey was collected using camera trapping.

Field sampling was conducted during the months of February 2021 to May 2021 wherein two separate camera trapping sessions were carried out. Western Rajaji (WR) was sampled from February 2021 to March 2021 followed by the deployment of camera traps in Eastern Rajaji (ER) during the period of April 2021 to May 2021. A total of 39 camera trapping stations were set up in WR while ER had 32 camera trapping stations. The camera traps were operational for an average of 33 days and 38 days in WR and ER respectively. However, since not all traps were working on all days due to equipment malfunctions, the total camera trapping effort in WR amounted to 1326 days while that in ER was 1222 days.

3.1.1 Study Design

To assist in even spacing between camera trapping stations, the study area was divided into grids of size 2km X 2km. Single camera traps, capturing only one flank, were deployed at a height of about 30cm - 40cm above the ground along animal trails, *raus* (dry seasonal drainages), forest roads and water holes in these grids. Sites for the placement of the camera traps were decided on the basis of presence of leopard and/or tiger signs such as scats, tracks, scrapes and scratches, as well as information gathered from the Rajaji Forest Department staff. This allowed in maximization of photographic captures of the desired species. Camera traps also captured images of potential prey during the sampling duration.

In accordance with the study design, most grids contained only a single camera trapping station. However, some regions of the park falling within the study area, were inaccessible due to the terrain and hence no camera traps could be deployed in such grids. Under these circumstances, an additional camera trapping station was set up in a nearby grid. However, it was ensured that no two camera traps were closer than 1.25 km to 1.5 km. At each camera trapping station, data was collected on the date of deployment and the camera ID. The location of the deployment station was also recorded using a handheld Garmin eTrex 20x GPS. The camera traps used (Cuddeback X-Change™, colour model) have a built-in passive infrared (PIR) sensor which is triggered by changes in the infrared radiation within the detection zone. An animal moving across, thus triggers the camera and a photograph is captured. Additional information collected by the camera trap and displayed on the picture includes date and time of the capture, the ID of the camera trap and the phase of the lunar cycle.

In WR, all deployed cameras were checked at least once and the data retrieved regularly to ensure proper functioning of the traps. However, in ER, only cameras deployed in Chilla range could be checked once. The others were revisited only at the time of retrieval at the end of the trapping period due to COVID-19 restrictions in place at the time of field sampling.

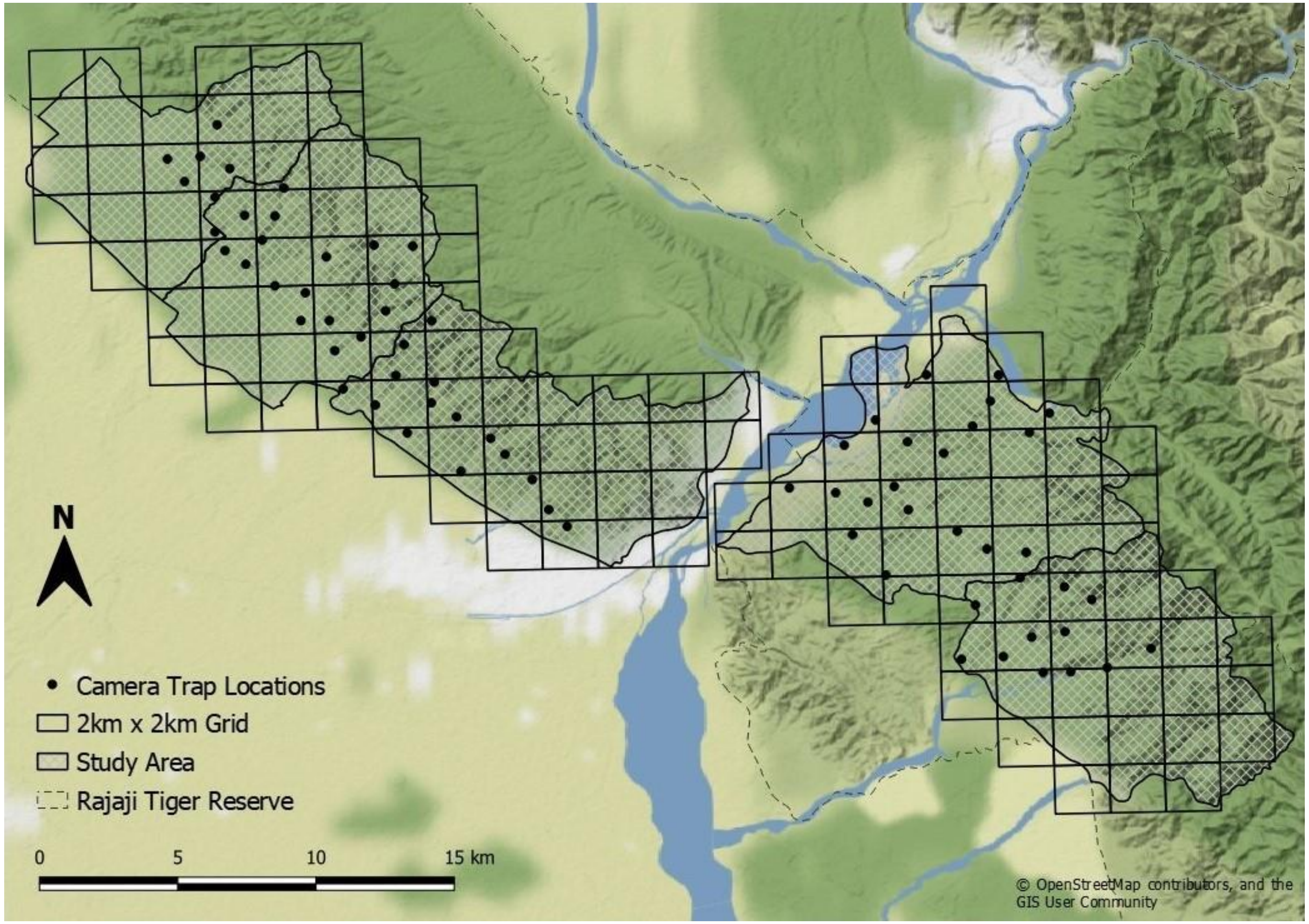

Figure 2. Map showing the study area with 2 km X 2 km grids and camera trap locations in Rajaji National Park.

3.2 Analytical Methods

All the photographs obtained from the camera traps were sorted up to the level of the species. This was followed by construction of record tables using the package camtrapR (Niedballa et al. 2016) in the software RStudio (R Core Team 2021). The minimum delta time, that is, time between two independent captures of the same species was set at 30 minutes (O’Brien, Kinnaird, and Wibisono 2003). Additional record tables were also constructed for leopards and tigers by individually estimating the time for independent photo-captures at 6 minutes and 8 minutes respectively.

Relative abundance index (RAI) was then calculated for the two felids and their potential prey species for all the camera trapping locations across Western and Eastern Rajaji. This was estimated by dividing the number of independent photo-captures of a particular species by the number of trapping days (that is, trapping effort) (O’Brien, Kinnaird, and Wibisono 2003). Cumulative values of RAI were subsequently calculated for big prey (chital and sambar), preferred prey (chital, sambar, barking deer, langur, macaque and wild pig) and all potential prey (chital, sambar, barking deer, cattle, hare, red junglefowl, Kalij pheasant, peafowl, porcupine, langur, macaque and wild pig) by adding the individual estimated RAI values (Krishnendu Mondal et al. 2011; Karanth and Sunquist 1995). These pooled RAI values were then used for further analysis.

3.2.1 Patterns in Space

Influence of Prey on Tiger and Leopard

The tiger and leopard RAIs were grouped into three categories each, namely low, moderate and high based on quartiles. Box plots were then constructed for these predator RAI classes against the RAI of both preferred prey and all prey in order to understand the influence prey relative abundances have on the relative abundance of predators. The plots were made using the package ggplot2 (Wickham 2009) in RStudio (R Core Team 2021).

Influence of Tiger on Leopard

The influence of relative abundance of tigers on that of leopards was also explored via construction of box plots between low, moderate and high categories of tiger RAI (based on quartiles), and the RAI of leopards. These too were constructed using the package ggplot2 (Wickham 2009) in RStudio (R Core Team 2021).

This relationship was further explored through a scatter plot between the tiger and leopard RAIs. This was constructed using Excel. Only leopard RAI values greater than zero and their corresponding tiger RAI values were plotted in order to avoid zero-inflation of the data.

Influence of Prey and Tiger on the Occupancy (Space use) of Leopard

Leopard space use was analysed using the occupancy framework. It involves a binary response (presence/absence) of a target species in a given spatial unit (e.g. grid). Detection histories are generated for the sampling location (camera trapping station) based on repeated surveys which are subsequently used to model for detection probability (MacKenzie et al. 2005). Site covariates such as prey availability, habitat, terrain, etc. are also used as predictors to model for detection as well as occupancy.

The current analysis was carried out using the software PRESENCE version 2.12.37. All camera trapping locations in WR as well as ER were used to model the occupancy of leopards. Presence matrices were generated manually using Excel and RAI of tiger, big prey and preferred prey were used as site covariates. Single season models were run and the best model chosen on the basis of the minimum AIC value.

Based on the results of the occupancy analysis, a map of space use by leopards in two sites, i.e. with and without tiger, was generated. This was achieved by assigning the occupancy estimates to the 2 km X 2 km camera trapping grids in both WR and ER using the software ArcGIS 10.6 (ESRI).

Activity Hot Spots of Predators and Prey and Segregation between Tiger and Leopard

Kernel densities for the three predator populations (tiger ER, leopard ER and leopard WR) and the prey populations in eastern and western Rajaji were estimated using the number of photo-captures of the respective species at a particular camera trap, and the duration of the trap's operation. The package camtrapR (Niedballa et al. 2016) in RStudio (R Core Team 2021) was utilised for this estimation. This was followed by the construction of 'heat' maps in ArcGIS 10.6 (ESRI) using the Kernel Density tool.

A map showing segregation in the activity hot spots of tiger and leopard in ER was also constructed by subtracting the kernel density surface of tiger from that of leopard. This was achieved using the raster calculator in ArcGIS 10.6 (ESRI).

3.2.2 Patterns in Time

Temporal Overlap Curves amongst Predators and between Predators and Prey

Diel activity patterns for each species were determined using the date and time stamps on the camera trap photographs. It is assumed that the number of camera trap records taken at different times during the day is correlated with the daily activity patterns of mammals (Linkie and Ridout 2011; Batschelet 1981). In order to reduce bias caused by repeated consecutive detections of the same individual of the same species, one record of each species per half hour per camera trap station was considered an independent capture, and subsequent records were removed (O'Brien, Kinnaird, and Wibisono 2003). The activity patterns were analysed using kernel density estimation curves. These are nonparametric estimates of the probability density function of distribution of independent captures which assumes that an animal is equally likely to be captured at any time as long as it is active (Linkie and Ridout 2011). Overlap coefficients between the daily activity patterns of predators as well as between predators and potential prey were estimated using the package overlap (Linkie and Ridout 2009) in RStudio (R Core Team 2021). Overlap coefficient (Δ) is defined as the common area under at least two temporal activity curves and it ranges from 0 (no overlap) to 1 (complete overlap) (Schmid and Schmidt 2006). Schmid and Schmidt (2006) proposed five general nonparametric overlap estimators (Δ_1 to Δ_5). For circular distributions, Δ_1 & Δ_2 are equivalent while the third, Δ_3 is unworkable (Ridout and Linkie 2009). Δ_5 on the other hand is unstable as small incremental changes in the data produce discontinuous changes in the estimate, resulting sometimes in estimates greater than one and hence is not useful (Schmid and Schmidt 2006). Therefore, overlap was computed using either the Δ_1 or Δ_4 estimator depending upon the sample size. If both samples were larger than 75, Δ_4 estimator was used whereas Δ_1 was used for small sample sizes (Linkie and Ridout 2011). The precision of the estimator was obtained through calculation of 95% confidence intervals (CI), as percentile intervals from 1000 bootstrap samples (Linkie and Ridout 2011; Meredith and Ridout 2014).

Influence of Tiger Visitation on the Visitation by Leopard at Camera Traps

To determine if temporal patterns of leopard are influenced by tigers at the same location, time lag between tiger and following leopard visits were measured. These were calculated manually through timestamps of images for all camera traps in ER having captures for both the species. A boxplot was then constructed between this lag time and the three tiger RAI categories namely low, moderate and high using ggplot2 (Wickham 2009) in RStudio (R Core Team 2021).

4. RESULTS

Western Rajaji registered a total of 4999 independent captures over the entire sampling period of 1326 trapping days. Eastern Rajaji, on the other hand, had 5677 independent records over 1222 days of camera trapping. A total of 28 mammalian species were recorded from WR while 27 were photo-captured in the eastern part of the Park. Mammal species found across both WR and ER include barking deer, chital, sambar, wild pig, elephant, black-naped hare, red junglefowl, Kalij pheasant, peafowl, langur, macaque, porcupine, palm civet, small Indian civet and rusty spotted cat. Nilgai was exclusively camera trapped in WR while hyena, black bear and sloth bear were only recorded from ER. Domestic prey included cattle in both the western and eastern sectors with additional captures of feral dog (n=1) in WR and feral cat (n=2) in ER. A total of 328 independent leopard captures were recorded in WR. ER, on the other hand, registered 233 independent tiger records but only 27 independent leopard captures.

4.1 Patterns in Space

4.1.1 Influence of Prey on Tiger and Leopard

An increase in the relative abundance index (RAI) of preferred prey resulted in an increase in the RAI of leopard. The tiger RAI though showed an initial increase with increase in preferred prey RAI, no clear pattern was observed between the moderate and high RAI classes in response to prey. (Figure 3.)

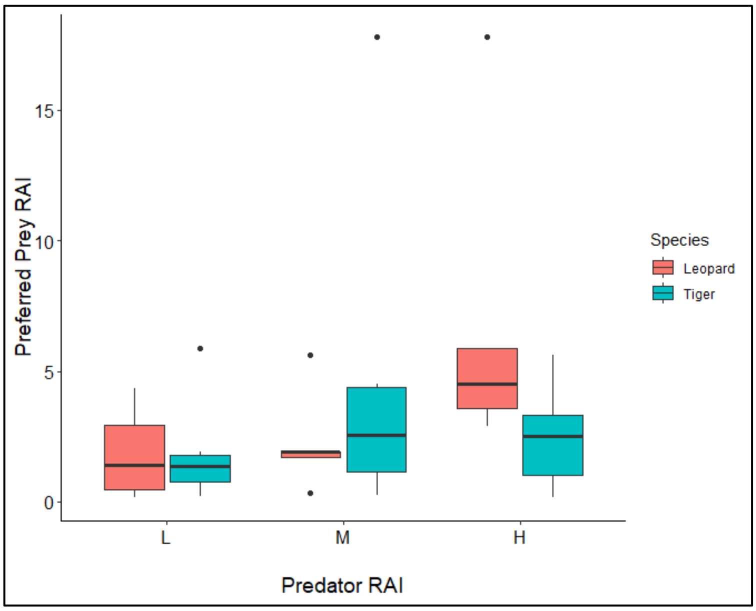

Figure 3. Box plot showing response of predators to increasing preferred prey relative abundance. The line within the box represents the median. L, M and H refer to low, moderate and high predator RAI categories respectively.

The pattern observed for the RAI of all prey species pooled together was similar to that seen for preferred prey RAI. Leopard RAI showed an increasing trend with increase in the RAI of all prey. The RAI of tiger increased initially but no decipherable pattern was observed between the moderate and high tiger RAI categories. (Figure 4.)

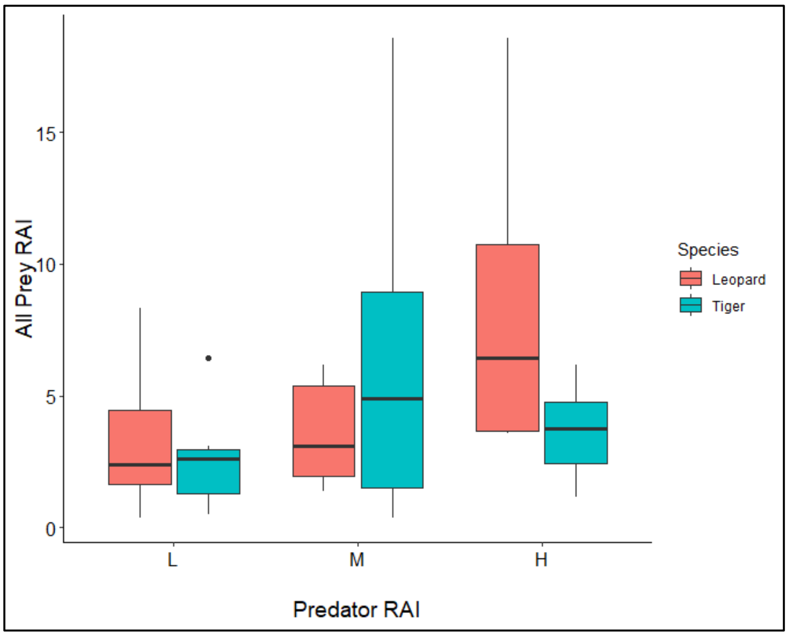

Figure 4. Box plot showing response of predators to increasing pooled relative abundance of all prey species. The line within the box represents the median. L, M and H refer to low, moderate and high predator RAI categories respectively.

4.1.2 Influence of Tiger on Leopard

Camera trap locations with low values of tiger RAI also showed low median leopard RAI values. As the tiger RAI increased so did the median relative abundance of leopard. However, with further increase in the RAI of tiger, a decline in the leopard RAI median was observed. (Figure 5.)

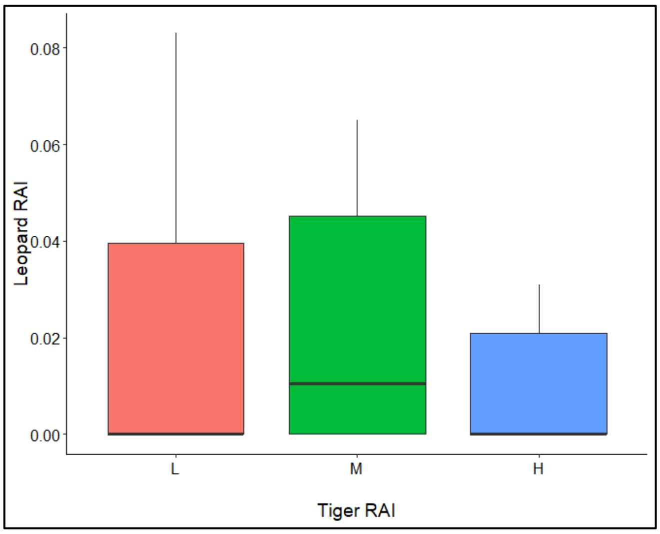

Figure 5. Box plot showing response of leopard to increasing relative abundance of tiger. The line within the box represents the median. L, M and H refer to low, moderate and high tiger RAI categories respectively.

A declining trend was observed for camera trap specific RAI of leopard with increase in tiger RAI. Only cameras with leopard RAIs greater than zero were plotted as multiple traps lacked leopard captures. (Figure 6.)

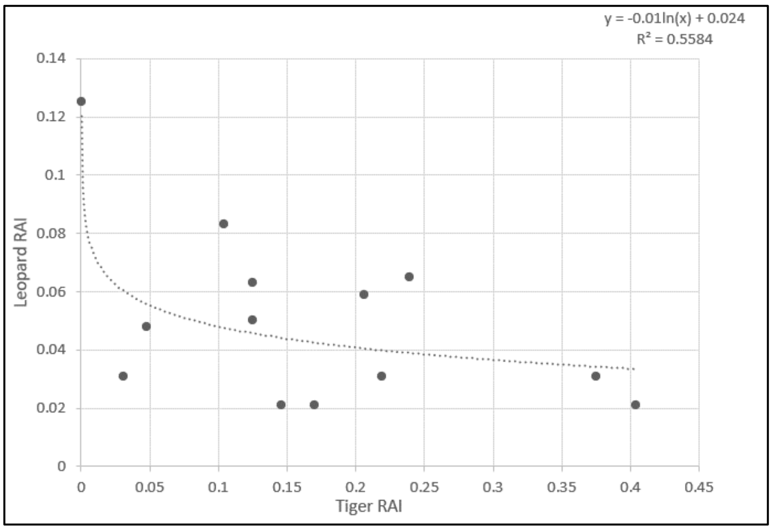

Figure 6. Scatter plot showing response of leopard to tiger RAI across the camera trap locations.

4.1.3 Influence of Prey and Tiger on the Occupancy of Leopard

Leopard occupancy was modelled across all camera trap locations (WR and ER) taking into consideration the influence of tiger RAI and the RAI of prey. The best fit model having the lowest AIC value resulted from the occupancy (psi) being influenced by the RAI of tiger. The relative abundance index of neither big prey (bprey) nor preferred prey (pprey) were found to be significant. (Table 1.)

Table 1. Occupancy models run for leopard incorporating the effect of the RAIs of tiger and prey. The best fit model with the minimum AIC value is listed at the top.

Model	AIC	deltaAIC	Number of parameters	-2*LogLikelihood
psi(tig),p(.)	1735.7	0	3	1729.7
psi(pprey+tig),p(.)	1736.07	0.37	4	1728.07
psi(bprey+tig),p(.)	1736.74	1.04	4	1728.74
psi(.),p(.)	1747.04	11.34	2	1743.04
psi(bprey),p(.)	1747.16	11.46	3	1741.16
psi(pprey),p(.)	1747.85	12.15	3	1741.85

The estimate of the naïve occupancy for the best fit model was 0.73. The occupancy of leopard for this model was found to be negatively influenced by the RAI of tiger. (Table 2., Figure 7., Figure 8.)

Table 2. Estimates for the best fit occupancy model for leopard.

Covariate	Estimate	SE
Psi intercept	1.79	0.40
Tiger RAI	-7.28	2.44
Detection intercept	-1.56	0.06

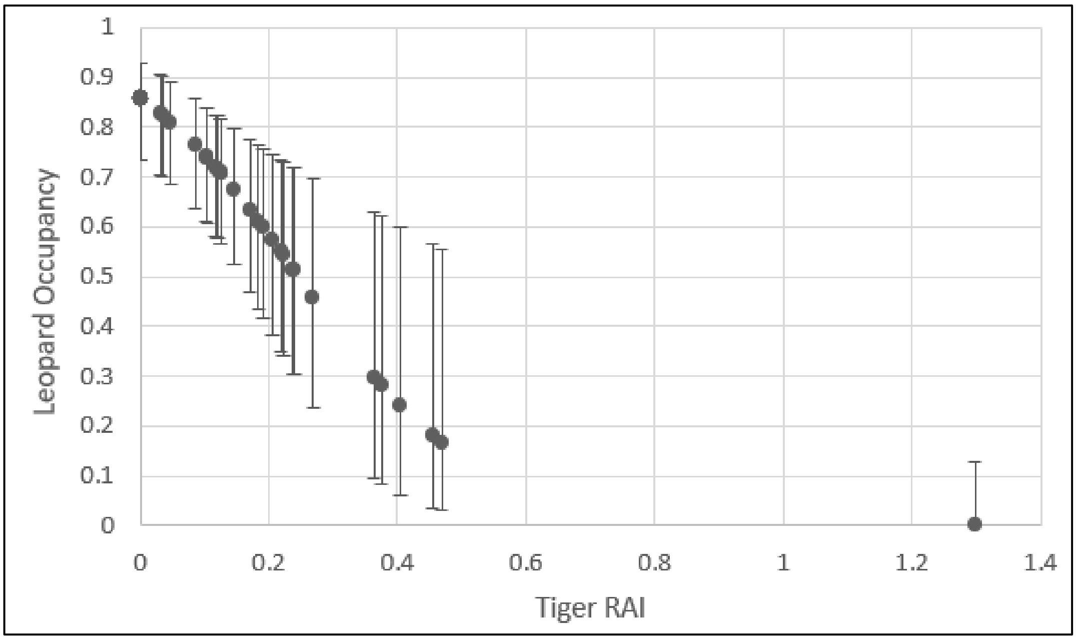

Figure 7. Plot showing negative relation between leopard occupancy (space use) and tiger RAI. The bars represent the estimated standard errors (SE).

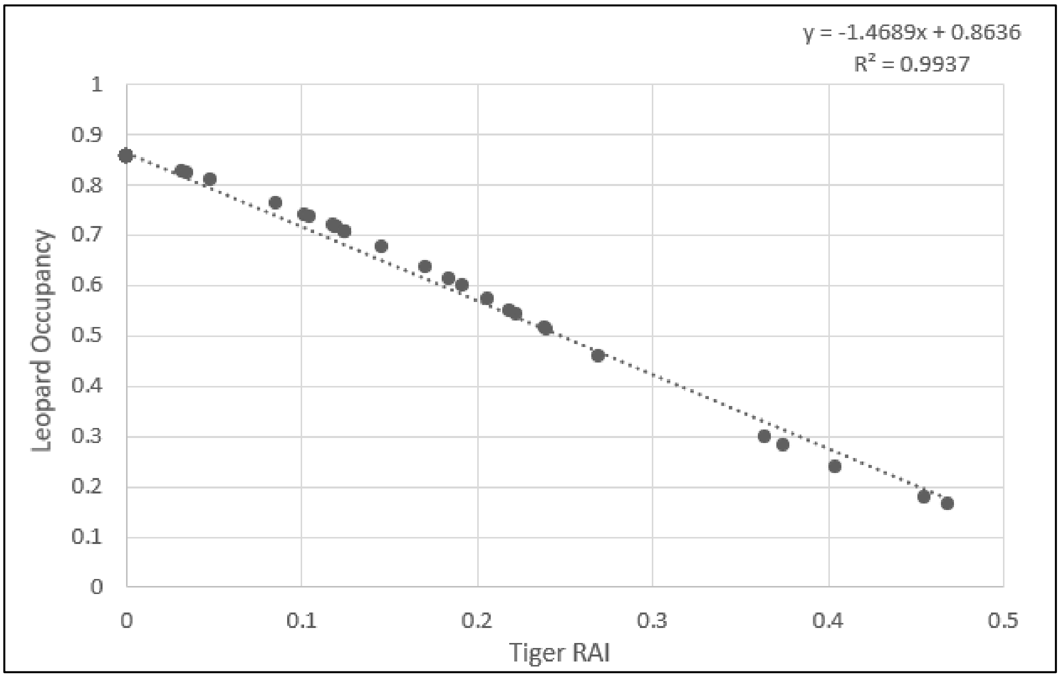

Figure 8. Plot between tiger RAI and leopard occupancy (space use) showing a linear negative relationship. The outlying point in the previous plot with tiger RAI equal to 1.297 has not been plotted here for clearer visualisation of the declining trend.

Grid-wise occupancy estimates of leopard for all camera trapping locations across the sampling ranges are shown in Figure 9. The estimates for occupancy of leopards were higher for Western Rajaji when compared to Eastern Rajaji.

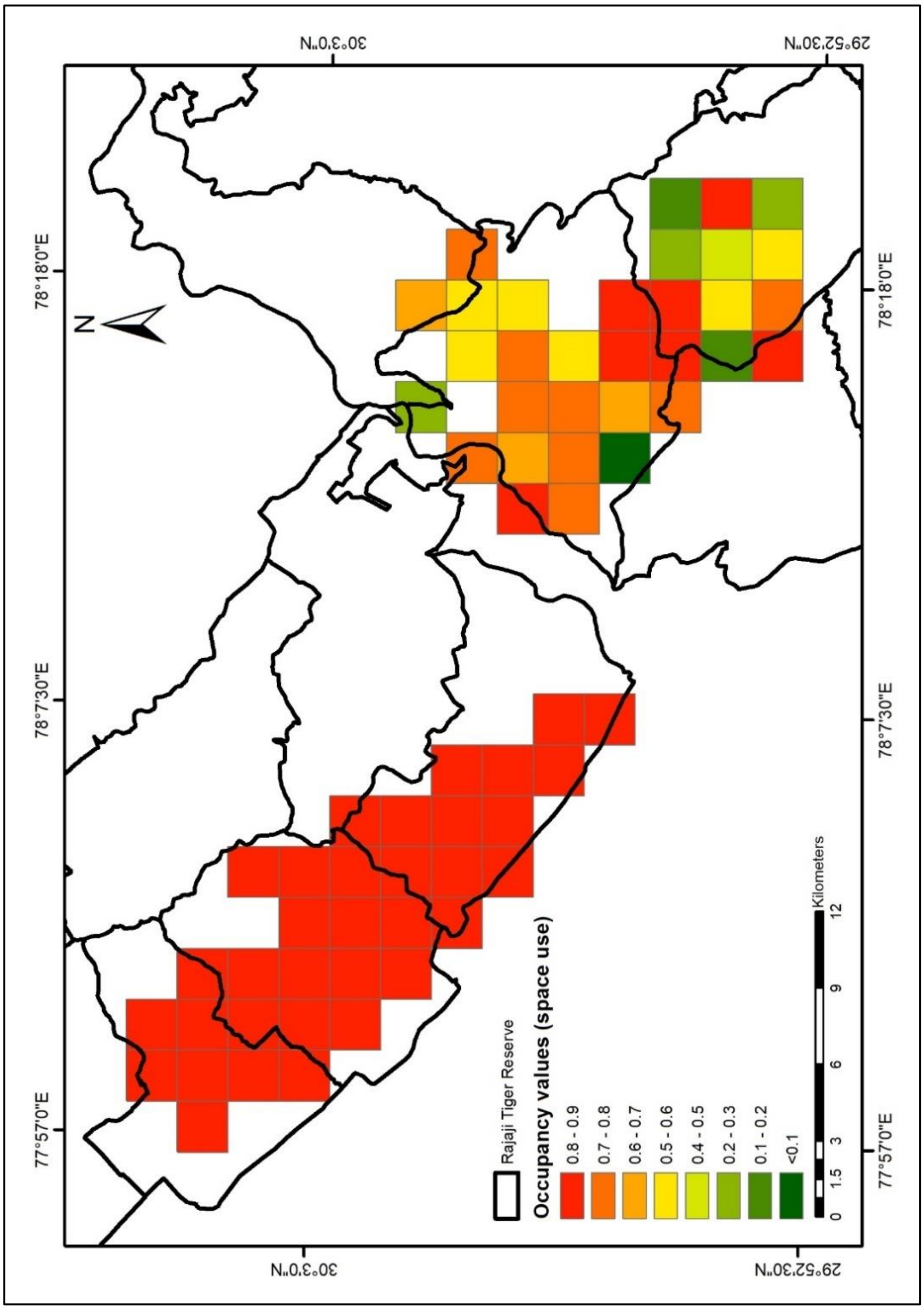

Figure 9. Map showing grid-wise leopard occupancy (space use) across the sampling area

4.1.4 Activity Hot Spots of Predators and Prey and Segregation between Tiger and Leopard

Leopard activity hotspots in ER were observed to be located closer to the fringe and peripheral areas of the park (Figure 10.) whereas most of the tiger activity in eastern Rajaji was localised towards the core regions (Figure 11.).

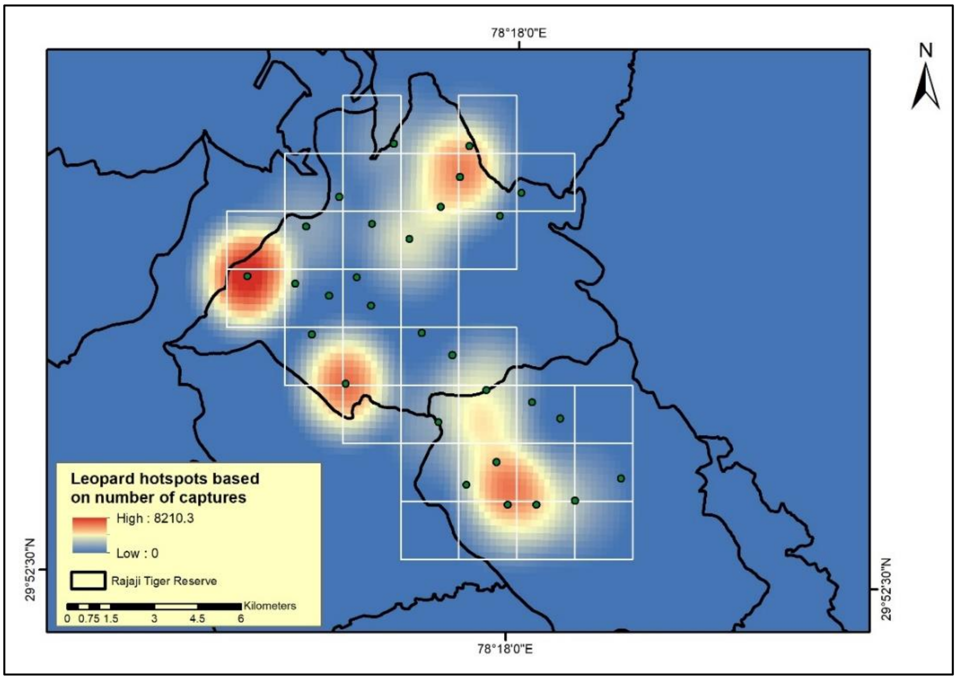

Figure 10. Map showing the activity hotspots of leopards in ER.

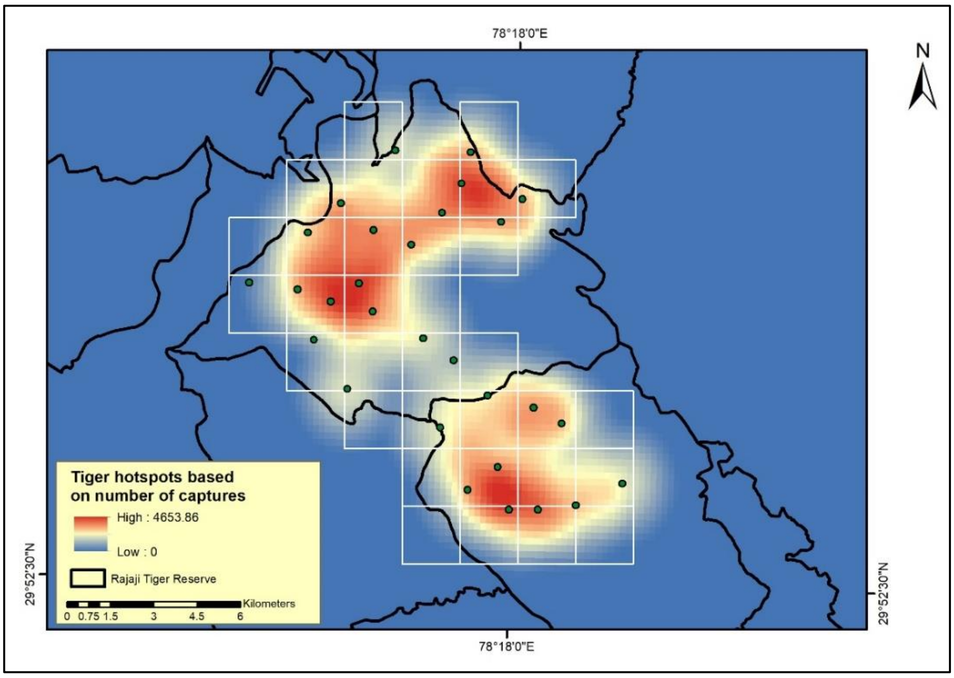

Figure 11. Map showing the activity hotspots of tigers in ER.

Upon construction of the segregation map, it was observed that the leopard activity hotspots differed from those of tigers, that is, high intensity tiger use areas were mostly not used by leopards. Some regions of overlap, however, were also seen between the two species. (Figure 12.)

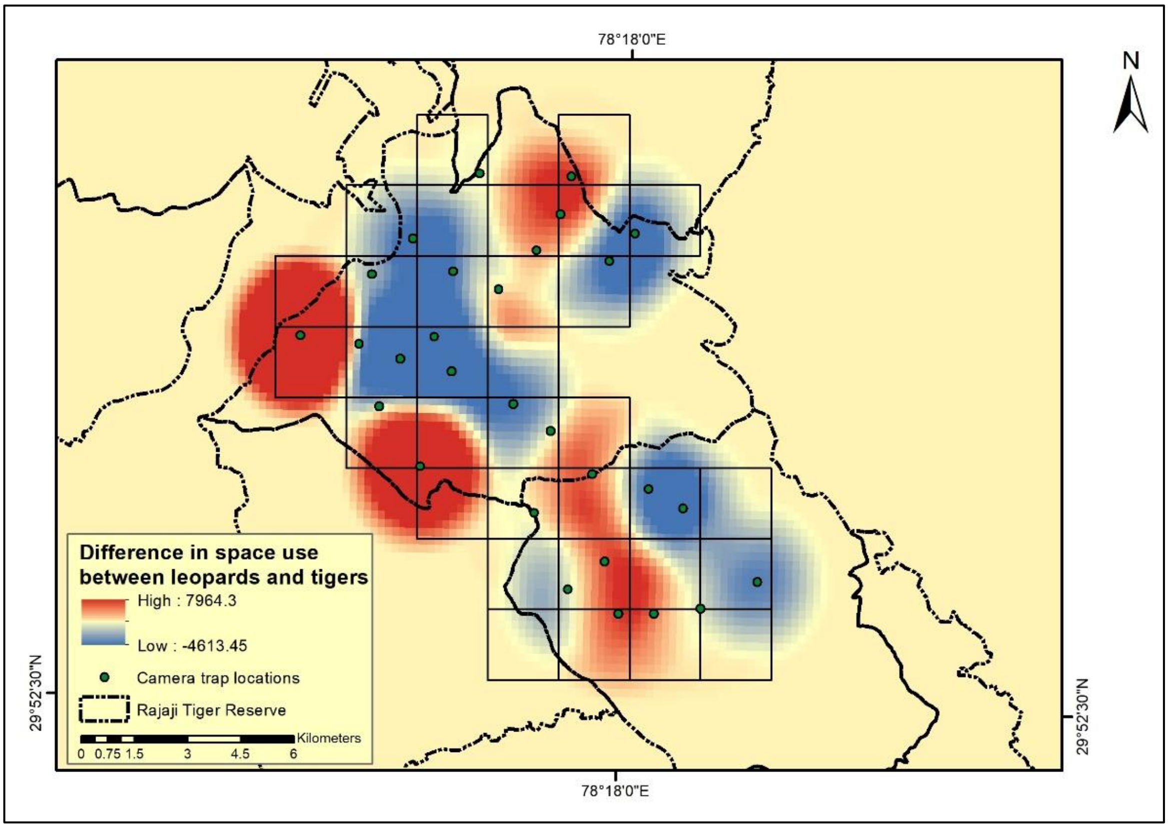

Figure 12. Map showing segregation in tiger and leopard activity hotspots in ER. The higher values (dark red shades) represent areas of more exclusive leopard usage while the lower values (dark blue shades) represent areas of more exclusive tiger usage. The intermediate values (lighter red and blue shades) are representative of areas of co-occurrence of the two felids.

Activity hotspots of preferred prey in ER were found to be distributed across the sampling area. The 'hot' areas for prey overlapped with those of co-occurrence of tiger and leopard in this region of the park and may explain, at least in part, the coexistence of the two large felids. (Figure 13.)

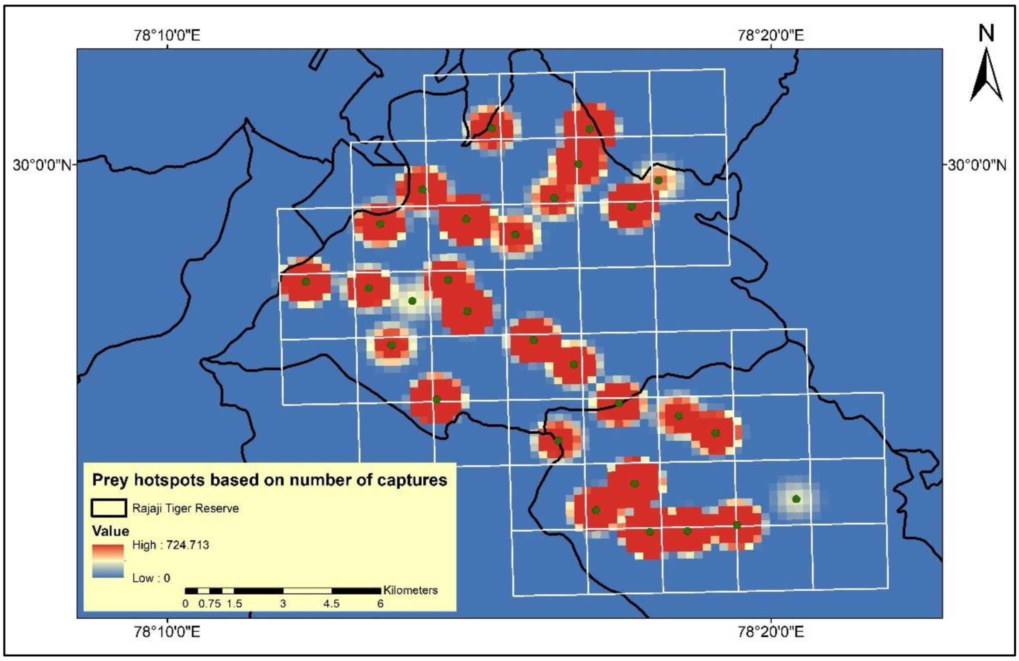

Figure 13. Map showing the activity hotspots of preferred prey in ER.

Leopards in WR showed activity hotspots distributed throughout the sampling area. This is indicative of maximisation in the usage of space in the absence of a more dominant predator. (Figure 14.)

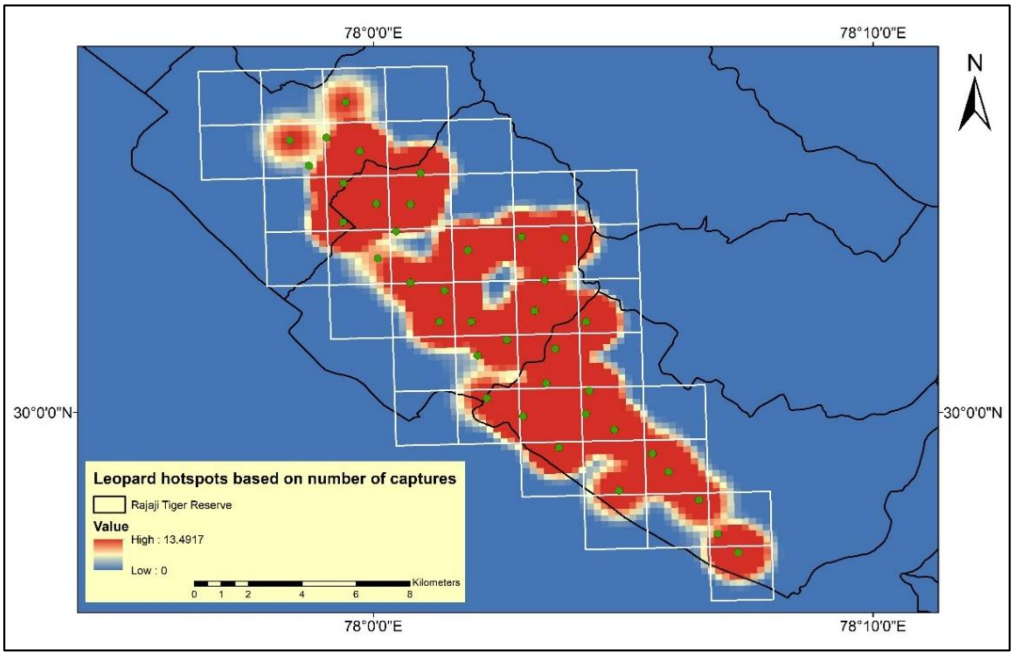

Figure 14. Map showing the activity hotspots of leopards in WR.

Preferred prey activity hotspots in WR were also found to be distributed throughout the sampling area (Figure 15.). This widespread availability of prey allows leopards to maximally utilise space in the absence of tigers.

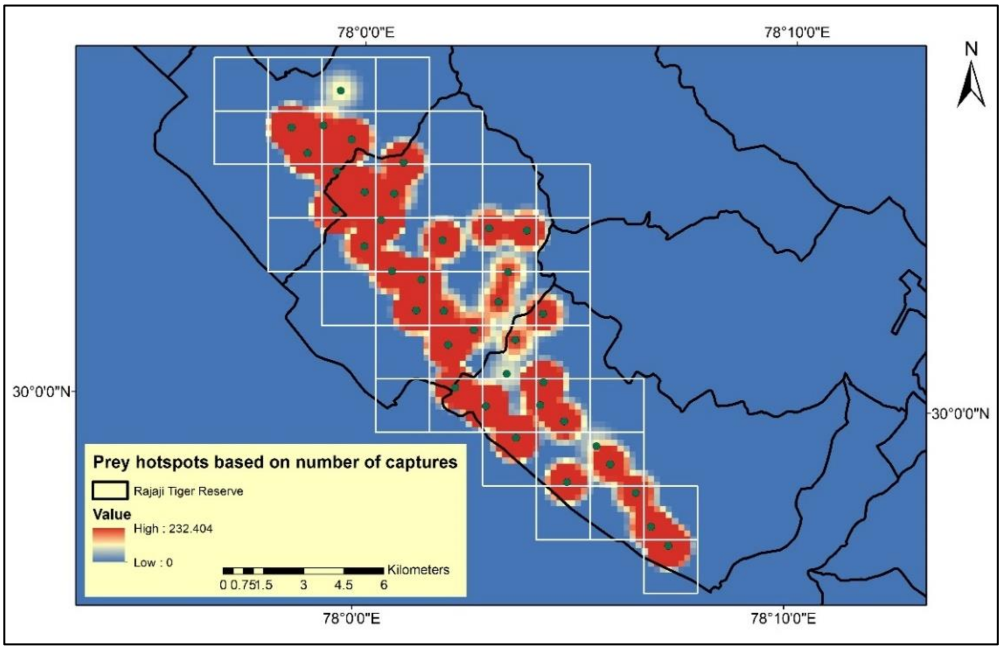

Figure 15. Map showing the activity hotspots of preferred prey in WR.

4.2 Patterns in Time

4.2.1 Temporal Overlaps among Predators

The temporal activity curves of the three predator populations (tiger in ER, leopard in ER and leopard in WR) were obtained as in Figure 16.

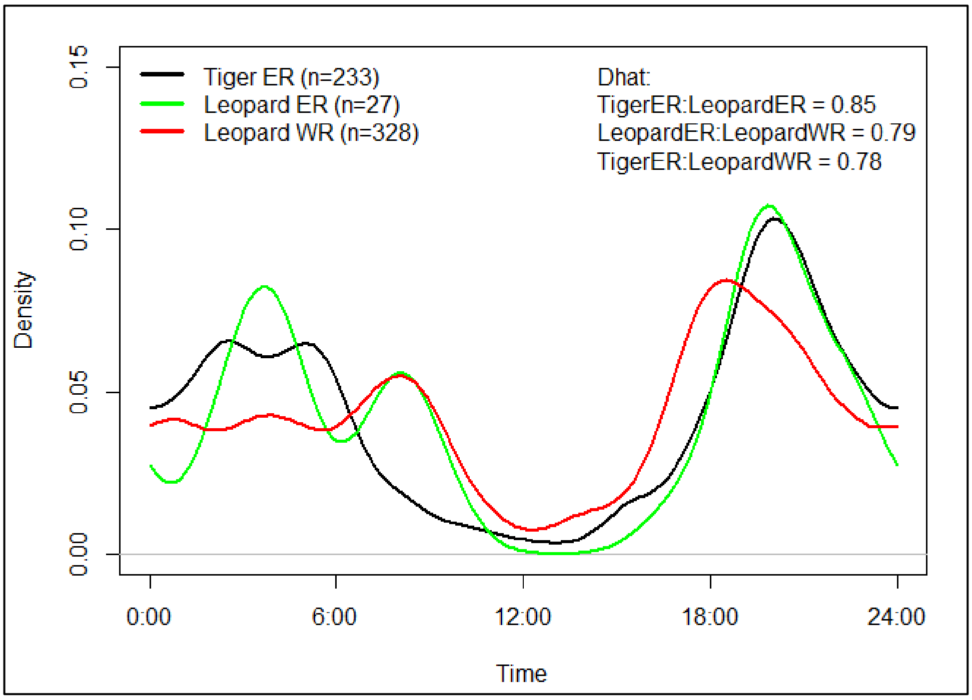

Figure 16. Plot showing temporal activity curves of the three predator populations. Values on the top right represent the overlap coefficients for the given predator pairs. 'n' denotes the number of photo-captures available to estimate the temporal curves.

A high temporal overlap was observed between tiger and leopard in Eastern Rajaji with an overlap coefficient (Δ_1) of 0.85 (0.73-0.94). Both species showed activity peaks during the dark period with declining activity during the day. While tigers only showed nocturnal peaks (black curve), leopards (broken red curve) also showed a smaller secondary peak in activity during the morning hours in addition to the two nocturnal peaks overlapping with tigers. This smaller peak coincided with decline in tiger activity during that period. (Figure 17.)

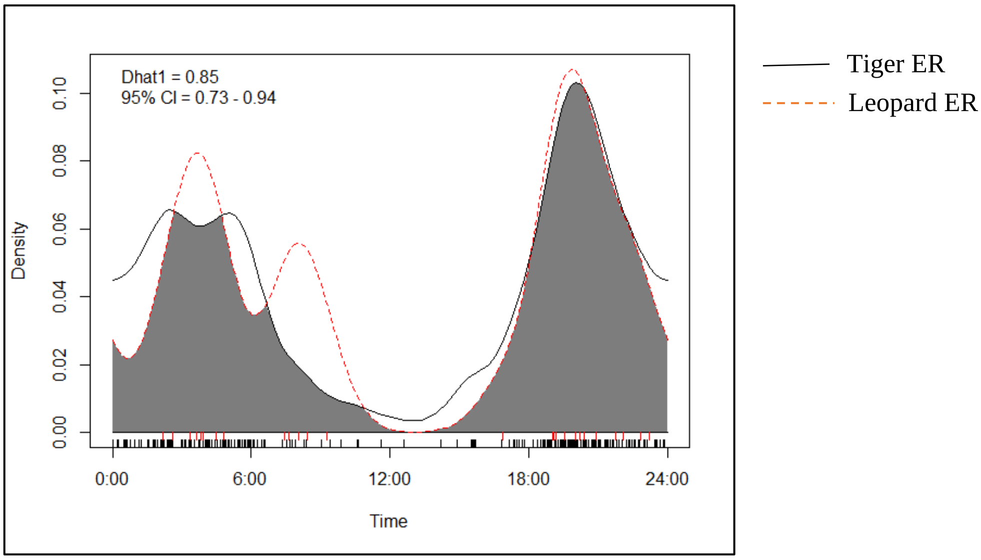

Figure 17. Plot showing overlap of activity patterns between tigers and leopards in Eastern Rajaji. Times of individual photographs are indicated by the short vertical lines above the x-axis (rug). The coefficient of overlap (Dhat1) is represented by the grey shaded area in the plot. The curve and rug lines indicated in black represent tiger while the red curve and rug lines represent leopard.

High temporal overlap was also observed between the WR and ER leopard populations with an overlap coefficient (Δ_1) of 0.79 (0.66-0.90). Leopards in WR (black curve) showed some level of activity throughout the day with peaks during the dark phase. The ER population (broken red curve), on the other hand, showed much lower activity during the day and higher peaks during the nocturnal phase. (Figure 18.)

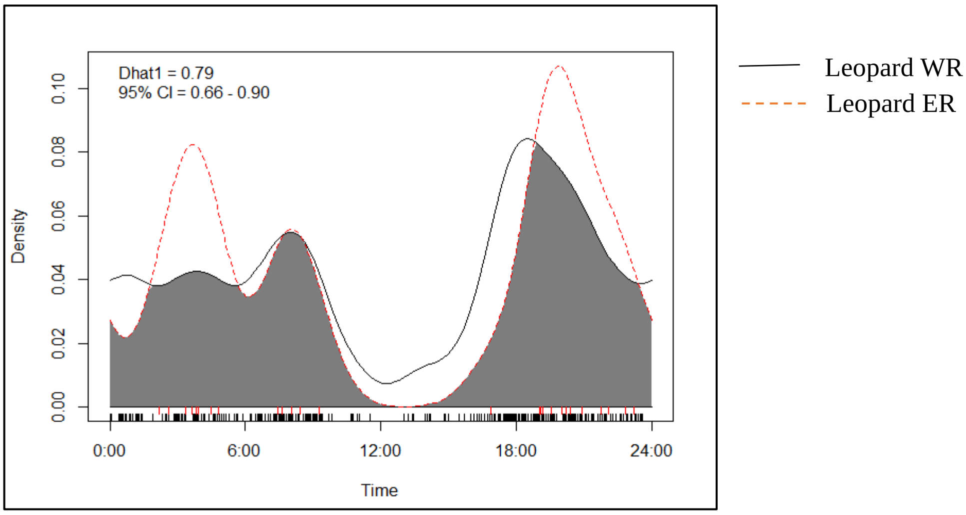

Figure 18. Plot showing overlap of activity patterns between leopards in Western and Eastern Rajaji. Times of individual photographs are indicated by the short vertical lines above the x-axis (rug). The coefficient of overlap (Dhat1) is represented by the grey shaded area in the plot. The curve and rug lines indicated in black represent leopards in WR while the red curve and rug lines represent those in ER.

High temporal overlap was observed between the tiger in ER and leopard in WR with an overlap coefficient (Δ_4) of 0.78 (0.71-0.84). The temporal curve for leopards was similar to that of tigers in that activity was spread throughout the day with two peaks. This is indicative of leopards demonstrating dominant predator-like activity in the absence of a more dominant predator. (Figure 19.)

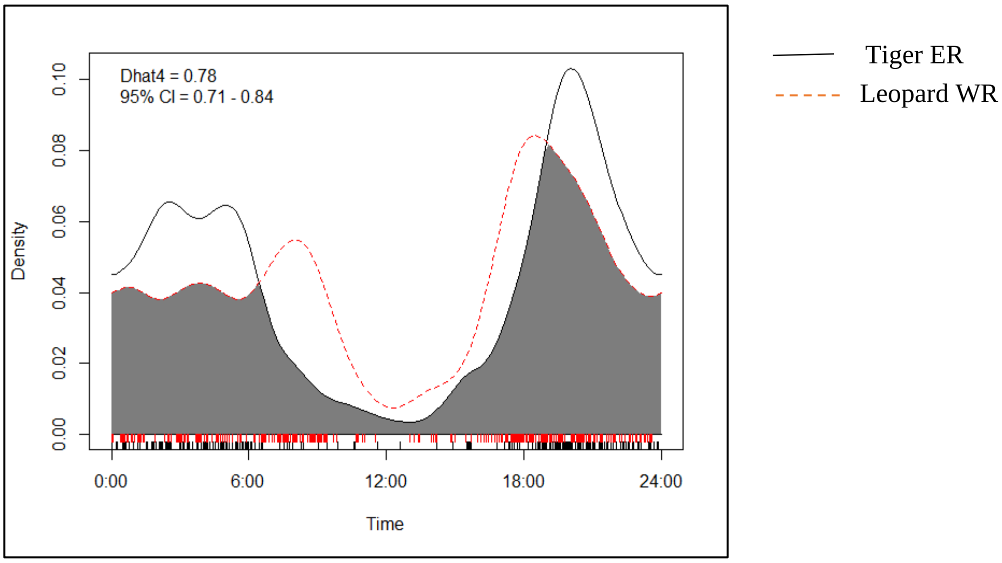

Figure 19. Plot showing overlap of activity patterns between tigers in ER and leopards in WR. Times of individual photographs are indicated by the short vertical lines above the x-axis (rug). The coefficient of overlap (Dhat4) is represented by the grey shaded area in the plot. The curve and rug lines indicated in black represent tigers in ER while the red curve and rug lines represent leopards in WR.

4.2.2 Influence of Tiger Visitation on the Visitation by Leopard at Camera Traps

It was observed that camera traps having low values of tiger RAI, that is, cameras with less number of tiger photo-captures and by extension locations less frequented by tigers, showed a high median lag time between leopard visits following tiger visits at the same trap location. As the RAI of tigers increased to the moderate category, lag time between tiger and leopard visits declined as is seen by reduction of the median value. However, as tiger RAI increased further to the high category, the lag time between tiger and leopard visits increased as is evidenced by more number of observations above the median in the third box plot (though the median decreased). (Figure 20.)

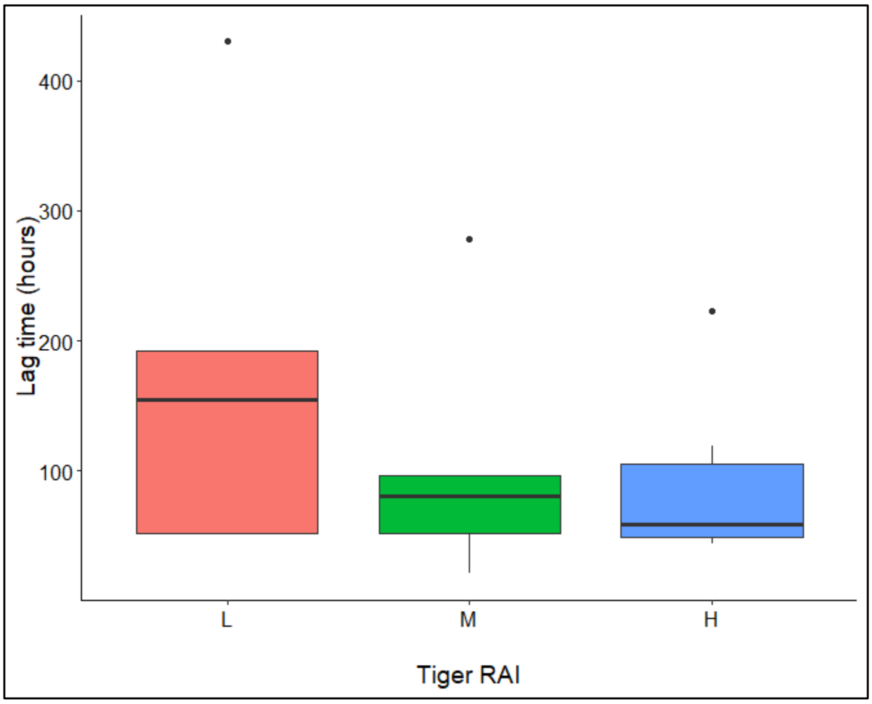

Figure 20. Box plot showing response of lag time between leopard visits at a camera trap following visits by tiger to increasing tiger RAI. The line within the box represents the median. L, M and H refer to low, moderate and high tiger RAI categories respectively.

4.2.3 Temporal Overlaps between Prey and Predators

Significant changes in the coefficient of temporal overlap of leopard and prey between Eastern and Western Rajaji were observed only for three prey species namely chital, sambar and wild pig (Table 3.)

Table 3. Coefficients of temporal overlap between predator and prey. Values in the parenthesis represent the 95% confidence interval limits.

	Tiger ER	**Leopard ER**	**Leopard WR**
Barking Deer	0.41 (0.32-0.49)	0.43 (0.27-0.59)	0.58 (0.50-0.67)
Chital	0.42 (0.37-0.48)	**0.45 (0.31-0.59)**	**0.67 (0.62-0.72)**
Hare	0.69 (0.57-0.80)	0.64 (0.47-0.79)	0.52 (0.45-0.59)
Red junglefowl	0.33 (0.27-0.41)	0.36 (0.21-0.52)	0.43 (0.37-0.49)
Kalij phesant	0.41 (0.31-0.51)	0.43 (0.27-0.59)	0.43 (0.35-0.50)
Langur	0.30 (0.24-0.37)	0.35 (0.21-0.49)	0.41 (0.29-0.53)
Macaque	0.26 (0.17-0.35)	0.28 (0.14-0.41)	0.34 (0.16-0.51)
Peafowl	0.36 (0.30-0.41)	0.39 (0.25-0.54)	0.47 (0.41-0.52)
Porcupine	0.60 (0.53-0.66)	0.53 (0.40-0.67)	0.55 (0.49-0.62)
Sambar	0.70 (0.63-0.76)	**0.63 (0.51-0.74)**	**0.85 (0.80-0.90)**
Wild pig	0.39 (0.32-0.46)	**0.42 (0.27-0.56)**	**0.81 (0.75-0.86)**

While temporal overlap coefficients changed significantly for three prey species, a change in the temporal activity pattern between WR and ER was observed only for sambar. In the western part of the park, the deer were active throughout the day with higher activity during the nocturnal hours whereas in ER they showed distinct activity peaks during the early morning and late evening hours. (Figure 21.)

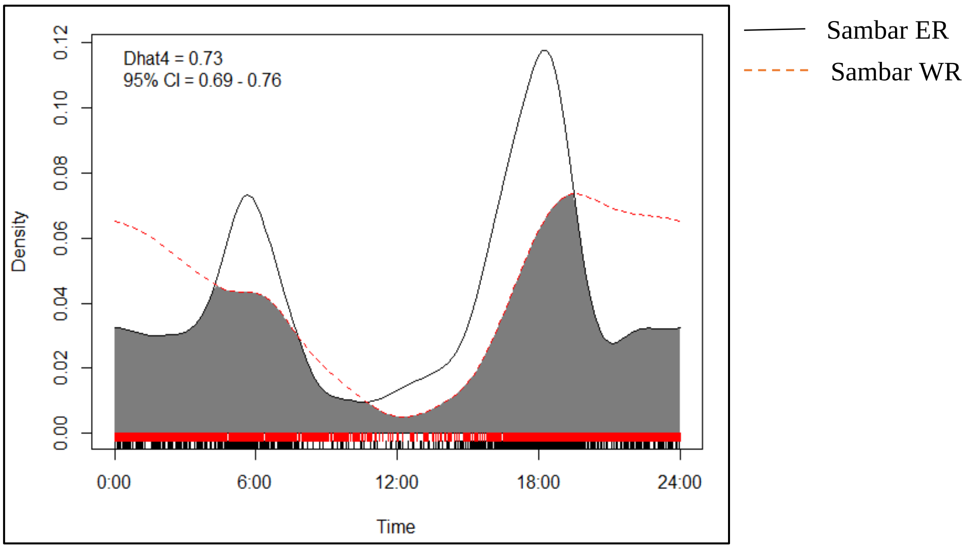

Figure 21. Plot showing overlap of activity patterns between sambar in ER and WR. Times of individual photographs are indicated by the short vertical lines above the x-axis (rug). The coefficient of overlap (Dhat4) is represented by the grey shaded area in the plot. The curve and rug lines indicated in black represent sambar in ER while the red curve and rug lines represent sambar in WR.

So as to incorporate the quantitative (Table 3.) and qualitative (Figure 21.) differences in prey activity patterns between WR and ER, temporal curves were plotted for preferred prey for the two regions of the park. It was observed that the activity of preferred prey was spread throughout the day in western Rajaji while prey in the eastern part of the park showed distinct peaks during the early morning and late evening hours. (Figure 22.)

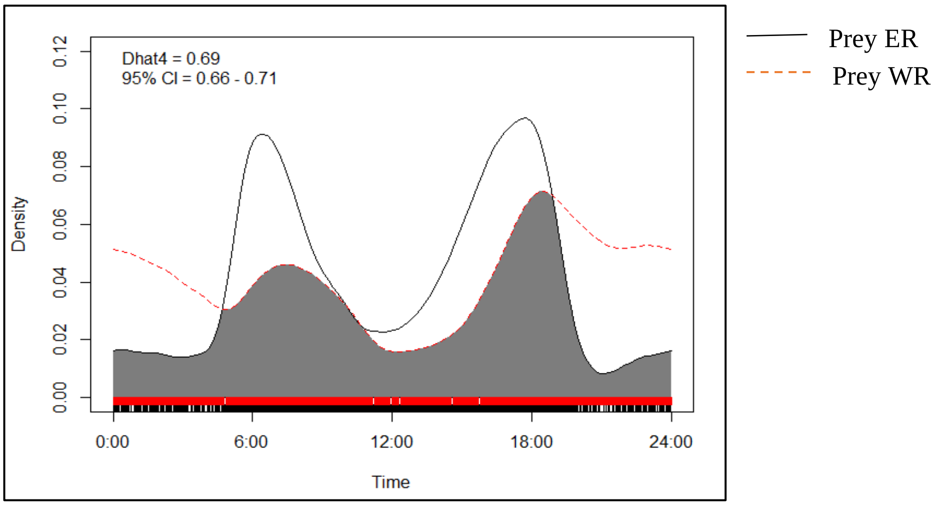

Figure 22. Plot showing overlap of activity patterns between preferred prey in ER and WR. Times of individual photographs are indicated by the short vertical lines above the x-axis (rug). The coefficient of overlap (Dhat4) is represented by the grey shaded area in the plot. The curve and rug lines indicated in black represent preferred prey in ER while the red curve and rug lines represent preferred prey in WR.

The temporal activity curves of the two predators in ER, that is, tiger and leopard, and that of the preferred prey were obtained as in Figure 23.

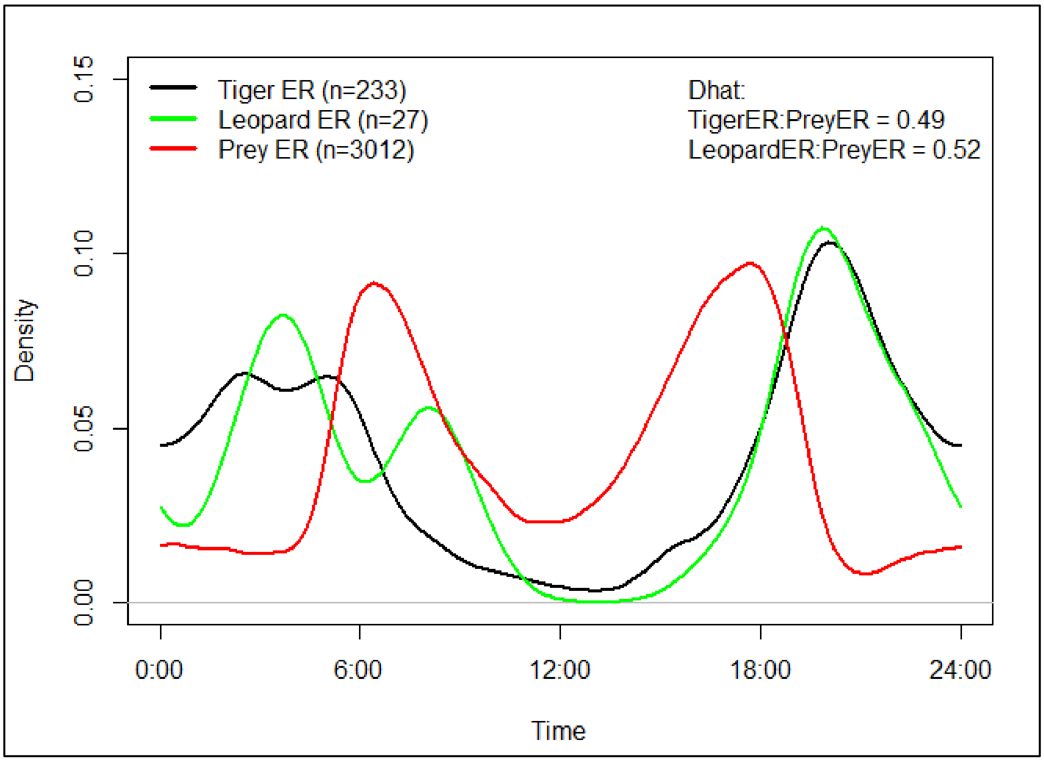

Figure 23. Plot showing temporal activity curves of the two predators and preferred prey in ER. Values on the top right represent the overlap coefficients for the given pairs of predator and prey. ‘n’ denotes the number of photo-captures available to estimate the temporal curves.

The coefficient of overlap (Δ_4) between the activity pattern of tiger in ER (black curve) and preferred prey in ER (broken red curve) was estimated at 0.49 (0.44-0.55). Prey showed some level of activity throughout the day with peaks during dawn and dusk. Portions of both the activity peaks of tiger overlapped with prey activity peaks. (Figure 24.)

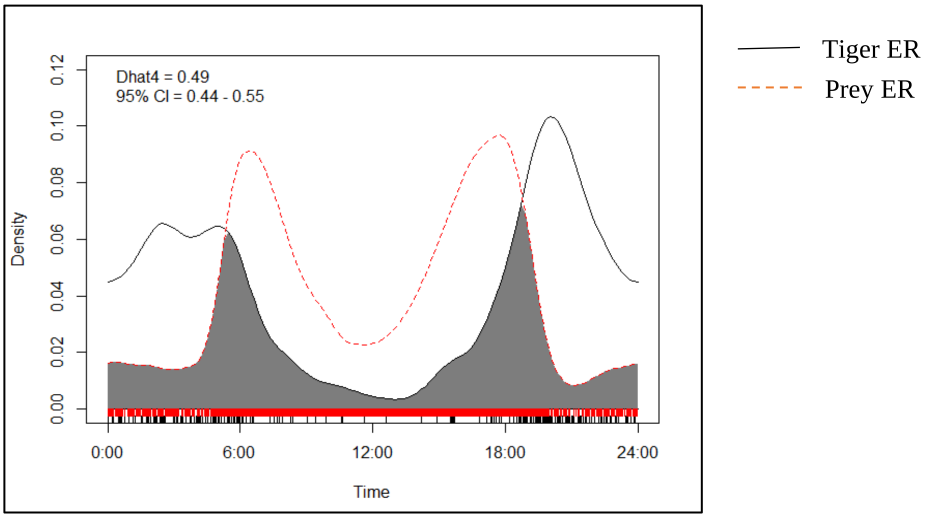

Figure 24. Plot showing overlap of activity patterns between tigers and preferred prey in ER. Times of individual photographs are indicated by the short vertical lines above the x-axis (rug). The coefficient of overlap (Dhat4) is represented by the grey shaded area in the plot. The curve and rug lines indicated in black represent tigers while the red curve and rug lines represent preferred prey.

The coefficient of overlap (Δ_1) between the activity pattern of leopard in ER (black curve) and preferred prey in ER (broken red curve) was estimated at 0.52 (0.37-0.64). Prey showed some level of activity throughout the day with peaks during dawn and dusk. The smaller secondary peak in the activity pattern of leopard coincided with the first activity peak of prey. The second peak for leopards partly coincided with the second prey activity peak. (Figure 25.)

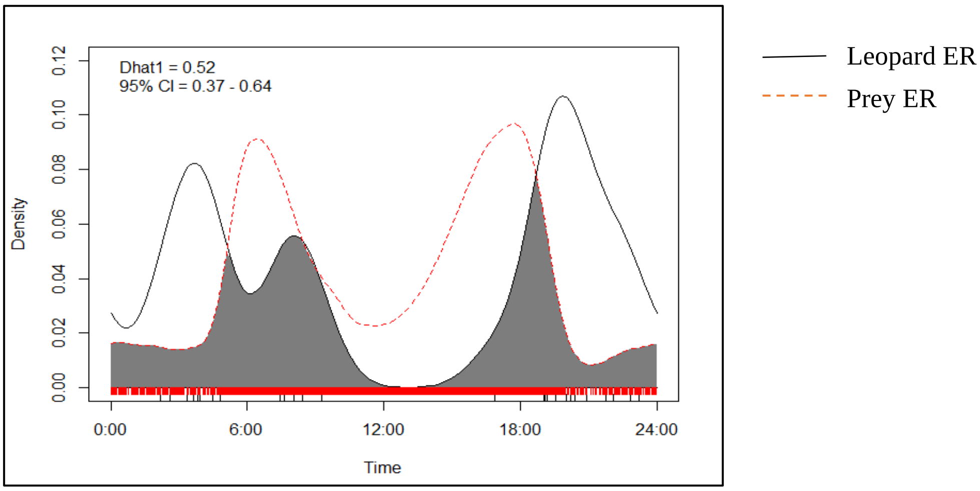

Figure 25. Plot showing overlap of activity patterns between leopards and preferred prey in ER. Times of individual photographs are indicated by the short vertical lines above the x-axis (rug). The coefficient of overlap (Dhat1) is represented by the grey shaded area in the plot. The curve and rug lines indicated in black represent leopards while the red curve and rug lines represent preferred prey.

The coefficient of overlap (Δ_4) between the activity pattern of leopard in WR (black curve) and preferred prey in WR (broken red curve) was estimated at 0.91 (0.86-0.94). Both predator and prey showed activity throughout the day with peaks for leopards during the dark phase. These activity peaks for leopard coincided with that for the prey. (Figure 26.)

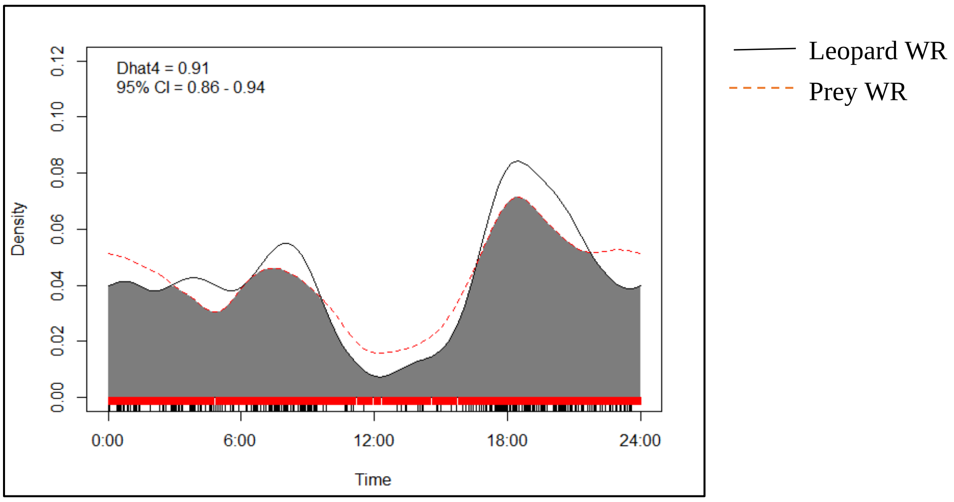

Figure 26. Plot showing overlap of activity patterns between leopards and preferred prey in WR. Times of individual photographs are indicated by the short vertical lines above the x-axis (rug). The coefficient of overlap (Dhat4) is represented by the grey shaded area in the plot. The curve and rug lines indicated in black represent leopards while the red curve and rug lines represent preferred prey.

5. DISCUSSION

The current study was aimed at understanding spatio-temporal patterns of leopards in the presence of a more dominant predator, tiger. Rajaji National Park serves as an excellent experimental ecological setup for this, as the western part of the Park hosts a leopard population but is devoid of tigers while both the large felids occur sympatrically in Eastern Rajaji. WR, therefore, acts as a control while ER serves as the experimental setup for this natural experiment. Additionally, since the study was conducted within the core area of the Tiger Reserve, disturbance due to human activities could be controlled for explicitly, as these may also lead to changes in spatial and temporal patterns of large felids thus incorporating bias in the collected data.

Leopards in WR function as the top carnivores owing to the absence of tigers. In ER, on the other hand, they are sub-dominant to their striped counterparts. Comparing and contrasting the two populations, thus, provides interesting insights into the functioning of dominance hierarchies among large felids.

The study found that leopards segregated themselves in tiger use areas in terms of space as well as time, at least in part. Leopard occupancy (space use) was found to be negatively affected by the relative abundance of tigers thus indicative of avoidance of high intensity tiger use areas by their sub-dominant counterparts. Some degree of segregation was also observed between leopard and tiger activity hotspots and regions of co-existence were attributable, at least in part, to the availability of prey in these areas. It was also found that leopards were unable to make use of entire available space in the presence of tigers, as opposed to maximisation in space usage observed in WR, the area of sole leopard occurrence. Differences in activity patterns were also observed for the two leopard populations with temporal curves showing distinct and pronounced activity peaks (3) in tiger dominated areas and having only a single peak with activity more spread throughout the diel in WR. In the case of the latter, leopard activity was found to be in tandem with that of prey in the absence of limitations imposed by a higher predator. Both predator and prey curves were spread throughout the day. On the other hand, in the presence of tigers, the smaller secondary activity peak for leopards during the morning hours segregated from that of the dominant predator while also being in tandem with prey. However, a high overlap was observed between the other peaks in tiger and leopard temporal patterns in eastern Rajaji. Hence, in regions of leopard and tiger co-occurrence, that is, in the absence of spatial segregation, and given the premise of high temporal overlaps, segregation between the two sympatric felids may be occurring at a rather finer scale. It may be a combination of spatial and temporal components wherein the two are never at the same place at the same time. This was evidenced by the lag between tiger and following leopard visits at camera traps in the study and may prove to be an important mechanism enabling sympatry between the two species of big cats.

5.1 Patterns in Space

When evaluating the influence of tiger on leopard, it was observed that at low values of tiger RAI, the RAI of leopards was also low as seen by the trends in the median values (Figure 5.). This may be attributable to low availability of prey in these areas, since the RAI of predators was also seen to be positively influenced by prey RAI (Figure 3., Figure 4.). With increase in the availability of prey, the RAI of tigers increases and is accompanied by an increase in the RAI of leopards. However, as the RAI of tigers increases further (from the moderate to the high category), a decline in leopard RAI is observed. Since the plot represents camera trap specific RAI values, the trend is indicative of differential spatial use between the two felids. Leopards do not frequent high intensity tiger use areas.

Prey resources (prey RAI) was also seen to influence the RAI of predators. With increase in the RAI of prey (preferred as well as all prey pooled together), an increasing trend was observed for the RAI of leopard. The RAI of tigers responded positively to prey RAI from the low to the moderate categories, however, a clear trend was not observed between the moderate and high RAI categories. This may be due to the study being conducted inside a protected area where availability of prey is high (chital:23.61/sq.km, sambar:10.61/sq.km, wild pig:8.22/sq.km, primates:12.92/sq.km) (Rathore H.S., 2015, M.Sc. Thesis) and thus no decipherable trend was observed.

In order to further analyse the relationship between the RAI of tiger and that of leopard, a scatter plot was constructed (Figure 6.). Camera traps having leopard RAI equivalent to zero (no photo-captures of leopards) were excluded in order to avoid zero-inflation of the data. A declining trend of leopard RAI was observed with increase in the RAI of tiger indicative of leopards avoiding camera trap locations (and by extension the areas) highly frequented by their striped counterparts. This trend is also indicative of spatial segregation between the two large carnivores.

To better understand the spatial patterns between tigers and leopards, space use was modelled using the occupancy framework as this corrects for detection, a factor not accounted for by relative abundance indices.

5.1.1 Spatial Patterns of Tigers and Leopards using Occupancy Framework

Leopard space use was found to be influenced by the RAI of tiger as per the best fit model with the lowest AIC value. Tiger RAI negatively influenced the occupancy of leopards, that is, areas with higher tiger RAI values showed lower leopard occupancy as opposed to regions with low RAI of tigers showing higher leopard space use. This is indicative of spatial segregation between tigers and leopards with the latter avoiding areas of high tiger usage. No significant relationship was found between leopard occupancy and the RAI of prey. This may be due to the study being conducted inside the National Park, as a result of which prey is abundantly available and there is a lack of any stark gradient in prey availability across the sampling area.

5.1.2 Segregation in Activity Hot Spots of Tigers and Leopards

The kernel density plots for the two predators in ER showed that leopards had activity centres distinct from those of tigers. This is indicative of spatial segregation between the two with the former avoiding high intensity usage areas of the latter. However, some regions of overlap were also seen between the activity hotspots of the two carnivores. This may be attributable to availability of prey in such regions thus allowing for co-occurrence. It is also possible that leopards in areas of overlap avoid tigers by using smaller forest trails as opposed to the major paths taken by tigers (Kawanishi 2002). Indeed, it may also so happen that while there are regions of overlap between the two, leopards never happened to be at the same place at the same time as tigers.

Upon comparison between the two leopard populations, it was also seen that their space use in the presence of tigers was rather restricted as opposed to maximisation in space utilisation by leopards in WR, that is, in the absence of constraint from a higher predator.

It was also observed that in ER hotspots of leopards were located closer to the fringes of the park while tigers had hotspots within the core region of the park. This is consistent with previous findings that sub-dominant predators may occupy sub-optimal areas in order to avoid the dominant predator (Chesson 1986; Rosenzweig 1991; Durant 1998).

While spatial segregation has been observed between tigers and leopards in previous studies such as the one carried out in Sariska Tiger Reserve (K. Mondal et al. 2012), exceptional patterns such as the one found in Mudumalai Tiger Reserve of tigers, leopards and dholes using the same areas (Ramesh et al. 2012) have also previously been seen.

In addition to the above findings, occupancy modelling showed a decrease in space use by leopards in ER when compared with that in WR (Figure 9.). Considering space occupied as a surrogate for population size, this pattern may be indicative of a smaller population of leopards in ER as opposed to WR. This is indirectly also reflected in the number of photo-captures of the felid, with only 27 independent records from ER when compared to 328 from the western part of the Park. This serves as a potential avenue for further research and may allow better understanding into the dominance dynamics at play between tigers and leopards in the Rajaji ecosystem.

5.2 Patterns in Time

The two species of sympatric large felids showed a significant high value of temporal overlap in ER (Figure 17.). Tiger activity pattern showed two nocturnal peaks and two of the three activity peaks of leopards in ER coincided with these. However, in addition to the minor differences in these two overlapping peaks of activity, a third activity peak of leopards was observed during the morning hours distinct from the temporal pattern of tigers in the region. This smaller peak coincided with the fall in the temporal activity of tigers in this period. Though studies such as the one carried out in Sariska, post the reintroduction of tigers, show distinct activity patterns between leopards and tigers and a clear temporal segregation between the two large felids (K. Mondal et al. 2012), studies from other parts of the country such as Mudumalai Tiger Reserve (Ramesh et al. 2012) and Manas National Park (Bhatt et al. 2021) demonstrate patterns similar to the current study. While some difference was observed in peaks of activity of tigers and leopards despite high overlaps in Manas National Park, no active temporal segregation was observed between tigers, leopards and dholes in Mudumalai Tiger Reserve.

Temporal overlaps were also plotted for the leopard populations in ER and WR in order to understand the deviation of their activity patterns in the presence and absence of tigers respectively (Figure 18.). While a high value of overlap was observed between the two curves, a closer inspection revealed some differences. Leopards in WR showed some level of activity throughout the day with two peaks in their activity patterns. The activity of leopards in ER, on the other hand, was confined to the nocturnal and morning hours with very little activity during the day. This felid population also showed three distinct peaks in activity with the two larger peaks having much greater intensity in comparison to the peaks at similar times for the WR leopard population.

It is, however, interesting to note that the peaks in leopard activity in ER distinct from that in WR (considered to be the native activity pattern of leopards as a result of absence of tigers) during the early dark hours and late evenings coincide with the activity peak of tigers in the area. In order to investigate this further, temporal overlaps of the predator populations in ER with that of prey activity patterns were analysed since the activity patterns of predators are often synchronised with those of their prey (Ramesh et al. 2012).

The temporal overlaps between leopards and individual prey species revealed quantitative differences between WR and ER for chital, sambar and wild pig (Table 3.) while differences in the activity patterns of individual prey only showed variation between the sambar populations in the two regions of the park (Figure 21.). To accommodate for both, the quantitative and qualitative differences, the photo-captures of the preferred prey species were pooled together and the temporal overlaps were analysed between these and the predators.

The activity pattern of leopards in WR was found to be highly synchronised with that of their prey. The temporal overlap between the two curves was estimated at 0.91 (0.86-0.94). The synchronicity of both, tigers and leopards in ER with their prey was much lower than that of the leopard population in WR. Portions of both the activity peaks of tigers overlapped in part with the peaks in prey activity. The activity peak for leopards during the late evening dark hours partly overlapped with the prey activity peak at dusk. The smaller activity peak during the morning hours, however, overlapped completely with the morning peak of prey. The early dark morning hour peak of leopards did not coincide greatly with the activity of prey and thus, this peak in leopard activity overlapping with tigers still remained unexplained.

It was subsequently observed that though leopards and tigers were photo-captured at similar time stamps in ER (as is evidenced by the temporal overlaps between the two), they were rarely at the same place (camera trap station) at the same time (Appendix 1). A lag was seen between tiger visits and following leopard visits. At low tiger RAI values, that is, areas less frequented by tigers, the lag between tiger and leopard visits was large. This may probably be an artefact of low abundance at such locations leading to only the occasional visits (Figure 20.). The lag time decreased when the tiger RAI was moderate. This is possibly due to rise in abundance and therefore, more frequent visitations at the camera trapping stations. However, an interesting trend emerged with increase in tiger RAI from the moderate to the high category. Lag time between tiger and following leopard visits at the same camera trap increased as is evidenced by greater number of observations above the median in the third box plot (though the value of the median decreased). Few leopard captures in ER (27) proved to be confounding to the analysis and a very significant pattern could not be observed. However, this is potentially worth future investigation and may yield interesting insights into finer scale segregation between the two species of large felids in the Rajaji ecosystem.

Caveats

The number of photo-captures of leopards from ER was low and only 27 independent records could be obtained during the entire sampling period. Spatial segregation of leopards may have led to this limited number of captures in tiger hotspot areas. A study design which encompasses larger areas with varying tiger and leopard densities may be useful in controlling for ‘photographic holes’.

Relative abundance indices (RAI) were used in exploring some relationship trends. These may show bias under a variety of circumstances: when there are differences in the detection between species, when home range sizes differ, and when there is change in detection over time thus masking true population trends (Sollmann et al. 2013). Hence, estimation of absolute abundances prior to analysis may yield more significant trends. However, since there were limited captures of leopards from ER absolute abundances were not computed.

The current study investigated resource partitioning among tigers and leopards along the spatial and temporal niche axes. Dietary niche segregation has previously been shown to be one of the major factors governing co-existence of sympatric large carnivores (Karanth and Sunquist 1995; Ramakrishnan, Coss, and Pelkey 1999; Hayward and Kerley 2008) wherein they avoid competition by hunting on different prey species (Seidensticker 1976). Thus, incorporation of partitioning along this axis may reveal a more complete insight into the ER system. The habitat may also play an important role as heterogeneity decreases chances of interaction between species thus reducing effects of dominance (Seidensticker 1976). This may also need investigation in the ER system. Dominant predators often also lead to a numerical response in the sub-dominant species as has been previously observed in Chilla range of Rajaji National Park (Harihar, Pandav, and Goyal 2009) and Sariska (K. Mondal et al. 2012). This may mediate coexistence between the sympatric felids by leading to reduction in the population of the less dominant predator and may also be the case in ER as very few leopards were photo-captured during the course of the study period.

The effect of many situational and managerial interferences could have also influenced photo-captures. During the course of camera trapping in WR several unforeseen events unfolded. Controlled burning was carried out by the forest department during the month of February 2021. The staff was also mobilised to track the reintroduced tigress as a result of which there was increased activity in the Park. Few forest fires also resulted in the month of March 2021. These might have contributed to disturbance to the leopard as well as prey population in WR.

6. CONCLUSIONS

Responses of a sub-dominant predator to the pressures exerted by a dominant counterpart constitute complex community interactions. Further research is required to better understand the dynamics of such responses. Studies need to be conducted in varying ecological setups along differing gradients of prey and predators in order to more completely explain these interactions. It becomes all the more imminent to understand the relative contributions of top-down and bottom-up mechanisms driving mesopredator patterns with the current global trends of apex carnivore decline. However, just as removal of top predators can have cascading effects on the mesopredators, so can their overinflation through focussed conservation management (Kumar et al. 2019). Hence, it becomes essential to look at and understand natural systems holistically, and strive to strike a balance through conservation practices.

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APPENDIX I

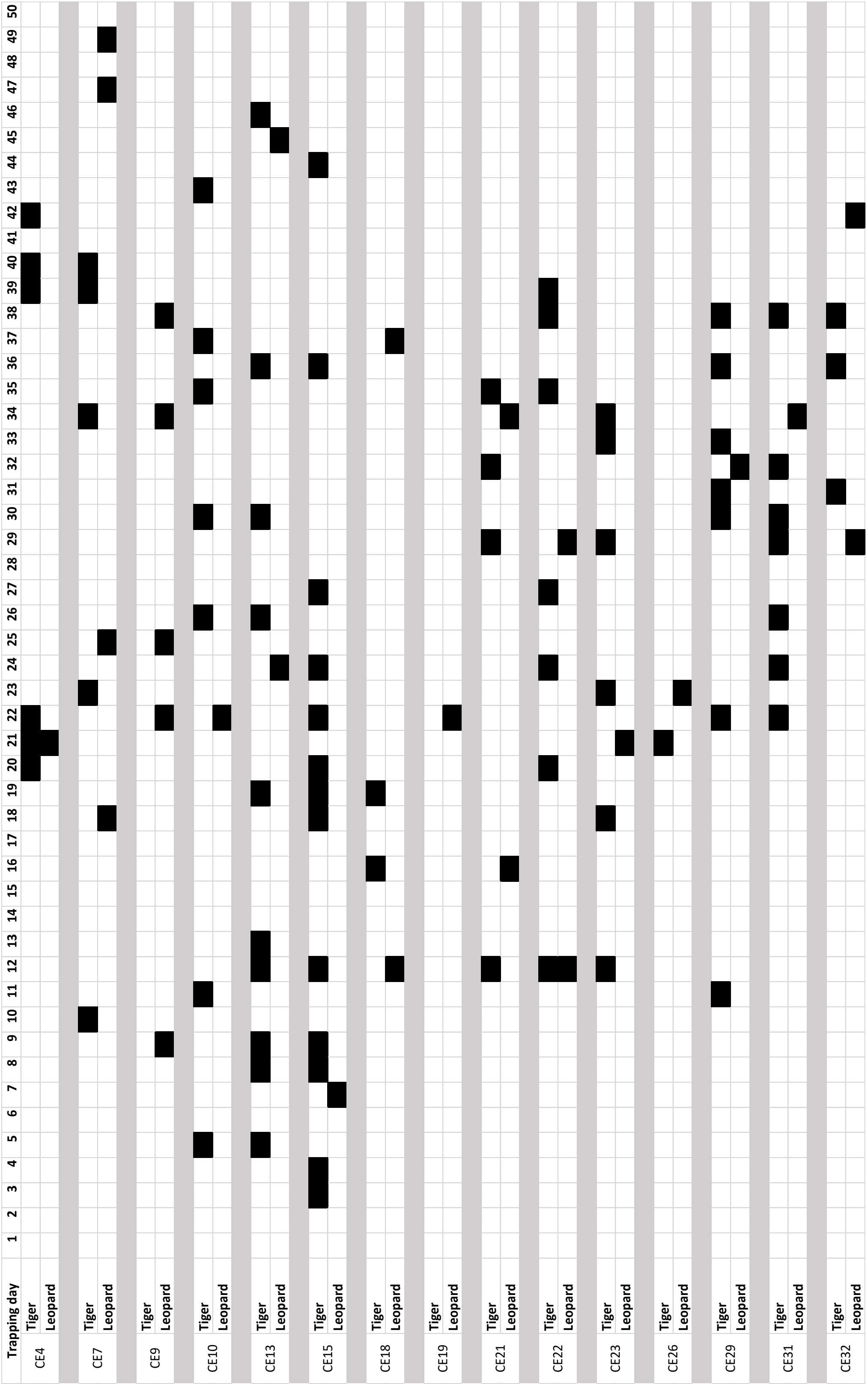

Figure 27. Pictorial representation of tiger and leopard visitation at camera traps. The boxes shaded in black represent at least one photo-capture of the species on the particular day.