RESPONSE OF LEOPARD (*Panthera pardus fusca*) IN VARYING DENSITY OF TIGER (*Panthera tigris tigris*) IN RAJAJI NATIONAL PARK, UTTARAKHAND

Thesis submitted for the partial fulfillment of

M.Sc. Degree in Wildlife Science

Saurashtra University, Rajkot

Harshvardhan Singh Rathore

Roll No. 13032900008

Supervisors

Dr. Bivash Pandav, Scientist E

Dr. Bilal Habib, Scientist D

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

CERTIFICATE

This is to certify that Mr. Harshvardhan Singh Rathore of Wildlife Institute of India has carried out an original research titled ***"Response of leopard (Panthera pardus fusca) in varying density of tiger (Panthera tigris tigris) in Rajaji National Park, Uttarakhand"*** in partial fulfilment of his ***"Master in Wildlife Science"*** from ***Saurastra University,*** Rajkot. This study was carried out under our supervision at the **Wildlife Institute of India** from December 2014 to May 2015. We also certify that this work has not been submitted for any other degree to any other university.

Bivash Pandav

Dr. Bivash Pandav
Supervisor
Scientist-E
Department of Endangered
Species Management

Dr. Bilal Habib
Co-Supervisor
Scientist-D
Department of Animal Ecology &
Conservation Biology

पत्रपेटी सं. 18, चन्द्रबनी, देहरादून-248001, उत्तराखण्ड, भारत
Post Box No. 18, Chandrabani, Dehradun-248001, Uttarakhand, INDIA
ई.पी.ए.बी.एक्स. :+91-135-2640111 से 2640115, फैक्स :0135-2640117
EPABX : +91-135-2640111 to 2640115, Fax : 0135-2640117
ई–मेल/E-mail : wii@wii.gov.in, वेब/website : www.wii.gov.in

ACKNOWLEDGEMENT

At the very outset, I take this opportunity to express my deep sense of gratitude to my Mamma and Papa as it is due to them I developed my interest in wildlife from the very beginning. I would like to thank the Director, Dean WII and Course Director XIV M.Sc. Wildlife Science for giving me opportunity to pursue my masters from this institute and carry out the present research work. I would like to express my sincere gratitude to my supervisors, Dr. Bivash Pandav and Dr. Bilal Habib for their constant support, guidance and encouragement throughout the process including all kind of obstacles in the earlier phase of the research work.

I owe my deepest gratitude to Dr. Y.V. Jhala and Prof. Qamar Qureshi for their unparalleled contribution toward the thesis work. The discussions which I had with them always led me on the right path and helped me to clear my ideas on the subject.

I fall in short of words when I come to express my gratitude towards Ujjwal sir and Neha mam. Their role in the completion of this work can't be expressed in words. They were always besides me when nobody else was and their presence always gave me strength and confidence to move towards the goal. All I can say is that this dissertation wouldn't have been possible without them. Thank You.

A special thank to Anup sir for always motivating me and for wonderful food and time we had under most stressful conditions. From the bottom of my heart I would like to thank the Uttarakhand Forest Department and field staff of Rajaji National Park for their kind assistance in field. I would like to thank Vadola ji, Digambar ji, Tishu Ji and whole staff of Ramgarh Range for some very memorable moments in the field. I would also like to thank Viwash, Anirudh, Akram, Luvprit, Nirdesh, Suvankar da, Prashant and Madhu for participating in the field work as without them it would have been a steep climb. The success of every project lies in team work. I would like to thank my team members Bisht ji, Annu, Ammi, Imam ji, Bhura Ji, Bashir and Ranjhu for giving their all in the field. I would also like to thank Nishant sir, Rutu ji, Ninad Sir, Sutirtha Sir, Bipin Sir, Rahul Da, Stotra Sir, Meghna Naitik, Urjit & Mohan for helping me in my analytical part and giving me valuable inputs on the subject. Finally, I express my special thanks to all classmates who remained helpful throughout the study. Thanks to all.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

Glossary of abbreviations

Rajaji National Park - **RNP**

Terai Arc Landscape - **TAL**

Tiger Habitat Blocks - **THB's**

Rajaji-Corbett Tiger Conservation Unit – **RCTCU**

Spatially Explicit Capture Recapture- **SECR**

Summary

Apex predators hold a special position in ecosystems due to their well known top down effects. Intra-guild competition is an integral process that affects population dynamics of large carnivores and may cause trophi c cascades. In India tiger and leopard are two large sympatric felids undergoing intra-guild competition. The two co-exist by segregating in their spatial, temporal and dietary niche. Rajaji National Park (RNP) provides an ideal condition to study interaction amongst large predators. Following human settlements relocation in the past decade, the tiger population has recovered in eastern RNP whereas due to lack of connectivity it has declined in western RNP. Thus, RNP provides a perfect ecological setup to study responses of leopard and prey in varying tiger density gradient. I assessed prey abundance in RNP using line transect based distance sampling using software Distance 6.2. Leopard and tiger density were also estimated by using camera trap pictures on a capture- mark recapture framework using spatially explicit capture- recapture models. Spatial separation was seen between the two carnivores by using density surface models. Principal prey, prey selection and their dietary overlap was also assessed. High abundance of major prey was seen with the density of chital ranging from 23.61±9.21 /sq.km in eastern RNP to 21.77±4.32/sq.km in western RNP and sambar ranging from 10.61±3.21/sq.km in eastern RNP to 15.65±2.52/sq.km in western RNP. The density estimates of leopard were 29.01± 4.00/100 sq.km and 25.37 ± 2.63/100 sq.km for the eastern and western sector respectively. The density estimates of tiger were 3.03±0.95/100 sq.km and 0.28±0.23/100 sq.km (only two tiger) for the eastern and western sector respectively. Leopard diet was primarily composed of chital in eastern RNP, in the western sector it was dominated by sambar. Chital was the principal prey species of tiger in RNP. Spatial separation was seen between tiger and leopard in both the sectors of the park with leopards clearly avoiding the high intensity usage areas of tigers. This study has created baseline data for predator and prey in RNP and would be helpful in managing the park better and for future monitoring.

1. Introduction

Carnivores occupy nearly every habitat available on the planet (Ripple et al. 2014) and the order carnivora has 287 existing species in 123 genera belonging to 16 families (Karanth & Chellam 2009). They have always been charismatic and draw human attention for varying reasons (Karanth & Chellam 2009). The carnivores of different sizes play an important role in regulating ecosystems (Prugh et al. 2009; Beschta & Ripple 2009; Estes et al 2011; Ritchie et al 2012). The intensity and strength of their impression relies on their size, density, metabolic needs, sociality and hunting style (Cardilla et al. 2004; Cardilla et al. 2005; Carbone et al. 1999). The studies worldwide have revealed that among terrestrial mammals several carnivore falls under the severely threatened group (Ceballos et al. 2005; Schipper et al. 2008). Large carnivores particularly are among the first order to disappear on habitat degradation (Hunter 1998). Anthropogenic factors like habitat loss and fragmentation, human persecution, decline in prey and utilization for medicine, fur etc have been the major cause of their reduction. It is their large energy requirements, slow life histories, existence at low population densities and need for large areas to forage for large prey which make them susceptible to clashes with humans which they barely cope up with (Woodroffe & Ginsberg 1998; Ripple et al. 2014).

Increase in the legalized protection, forest expansion, prey population recovery and reintroduction programmes have led to the rise in population of some carnivores like Cougars (*Puma concolor*), Brown Bear (*Ursus arctos*), Wolves (*Canis lupus*) and Lynx (*Lynx lynx*) (Breitenmoser 1998; Swenson et al. 1998; Linnell et al. 2001). Large carnivores especially the top predators are the keystone species as they affect ecosystems through top-down effects (Ripple & Beschta 2006; Ripple & Beschta 2007; Dalerum et al. 2008; Owen-Smith & Mills 2008). Ecological impact of large carnivores is noticeable even at low densities (Wallach et al. 2010). The top predators were previously perceived of having their cascading impacts only on herbivores and plants in the food web. It has been learnt that they exert their controlling effects on other species such as meso-carnivores (Morrison et al. 2007; Ritchie et al. 2009; Ripple et al. 2014). Thus, top predators have dual contribution of restricting large herbivore population via predation and meso-carnivores through intra-guild competition. It shapes the ecosystem by multiple network of food-web. As a whole it forms the foundation on which the stability and strength of the ecosystem functioning lies upon (Ripple et al. 2014).

One of the crucial ecological processes affecting the population dynamics of top predator guild are intra-guild competition and predation (Palomeres & Caro 1999, Linnell & Strand 2000, Caro & Stoner 2003). In sympatric large carnivore guild the superior species may be responsible for making a competitively inferior species rare in an area (Palomeres & Caro 1999; Caro & Stoner 2003) and may even lead to its extinction (Vucetich & Creel 1999). As top predators are highly vulnerable for extinction, the understanding of ecological relationships and co-existence in the large carnivore guild is extremely important in today's conservation oriented era (Purvis et al. 2000). Further, the boom in human population has further added pressure on the small sized reserves (i.e. reserves which are smaller than naturally functioning ecosystem, which are quite common) (Hayward & Slotow 2009), resulting in habitat declination. Its alteration leads to transformation in resource availability that affects predatory as well as competitive interaction dynamics (Ritchie & Johnson 2009). Thus, this coercive shoving of top predators in much smaller areas increases the intensity of hostile interactions among them which may stimulate the extinction process (Creel 2001, Caro & Stoner 2003). Active management is required for these naturally deficient ecosystems (Walters 1986).

Carnivores are affected by competition from other guild members (Mills & Mills 1982; Johnson and Franklin 1994; Karanth and Sunquist 1995; Palomares et al. 1996; White and Garrott 1997). There are five forms in which competition may take place among carnivores (Creel et al. 2001):

(1) Avoidance among carnivores through visual or olfactory contact.
(2) Active avoidance which results in shifts in habitat usage. It may also reduce foraging efficiency of the inferior species (Lima & Dill 1990).
(3) Exploitative competition takes places when similar food resources are shared by predators. Greater abundances of apex predators can lead to the reduction of food available to smaller sympatric carnivores.
(4) Kleptoparasitism (Food Stealing) is another form of competition. It increases the time costs and raises the risks associated with hunting as it is required to fulfill the demands of the additional food being lost to the other (Caro & Stoner 2003).
(5) Inter-specific killing or intra-guild predation (Polis & Holt 1992) may limit the abundance and distribution of some carnivores (Laurenson 1995; Lindstro¨m et al. 1995). It is known to

affect densities of species two to three trophic levels far-off from the killing carnivore (Palomares et al. 1995; Crooks and Soule′ 1999).

The inter-specific competition among carnivores is one of the most important systems that restrict the total species number occupying an assemblage due to their resemblance in the ecological niches (Di Bitetti et al. 2010). The inter-specific competition in carnivores usually increases when the diet schemes and adaptations of morphological features are similar (Morin 1999). Reduction in densities, growth, fecundity and altered age structure at population level are the outputs observed as a result of intra-guild competition (MacNally 1983; Petren and Case, 1998). The intensity of the inter-specific competition is more among the larger carnivores than in the smaller carnivores as there is lot more difficulty in capturing the larger prey which also correspond to a large amount of food and is valued to be stolen and defended (Xiaoming et al. 2004). The species with common resource demands have co-evolved to minimize competition (Ramesh et al. 2012). The coexistence of morphologically alike species and avoidance of inter-specific competition is attained by behavioral mechanisms like spatially and temporally segregating their activities (Pianka 1974, Schoener 1974a, Durant 1998, Linnell and Strand 2000, Harrington et al. 2009). The formation of groups also allows the medium as well as small sized carnivores to develop anti-predator strategies and fight more effectively for resources (Eaton 1979; Lamprecht 1981; Gittleman 1989).

The other ecological factors like specificity of the habitat, the specialization in prey of varying sizes also contributes to the coexistence of sympatric large carnivores (Ramesh et al. 2009). The abundance of ungulate is the major factor governing carnivore abundance (Carbone & Gittleman 2002). High densities of apex predator lead to higher encounter rates between them and sub-ordinate carnivores, which compel the latter to avoid the sites (Ramesh et al. 2012). Habitat structure or habitat heterogeneity affects the intensity of predator-prey interactions (Persson & Eklov 1995; Langellotto & Denno 2004). It is equally applicable to the sympatric large carnivore guild (Warfe & Barmuta 2004; Harvey & Eubanks 2005; Finke & Denno 2006, Griffen & Byers 2006). Food supply generally limits the carnivore populations (Macdonald 1983). Large carnivores separate themselves in the food requirement on the basis of their body size, hunting behavior, social organization, time of activity, habitat use and principal prey. Thus, the dietary niche separation is one of the major mechanisms governing the co-existence between large sympatric carnivores (Karanth & Sunquist 1995; Ramakrishnan et al. 1999; Hayward & Kerley 2008).

In this age of extinctions it becomes really important to keep the whole guild of large sympatric carnivores intact as maintaining predator richness is essential for functioning of natural ecosystem (Bruno & Cardinale 2008). In various parts of the world reintroduction programmes of carnivores to refill the areas with whole set of indigenous fauna are being planned and implemented. It needs sound knowledge of carnivore ecology and their guild for successful operations (Hayward et al. 2007a; Finlayson et al. 2008). Top carnivores are reintroduced for their conservation in their natural habitat like tiger reintroduction in Sariska Tiger Reserve in India (Sankar et al. 2010) or for the economic growth, GDP and development of the country like lion reintroduction in 37 reserves of South Africa (Slotow & Hunter 2009). The reintroduction or extinction of large carnivores may cause very prominent effects on the structure of ecosystems through trophic cascades and meso-predator release respectively (Ray et al. 2005; Schmitz et al. 2006; Ripple & Beschta 2007; Carpenter et al 2008). Complete understanding of top-down processes of a large carnivore guild is not well known (Finke & Denno 2005) and the knowledge of incomplete guild functioning (i.e. effect of removing one of the components from the guild) is also lacking which is important when we are losing our large predators (Hayward & Slotow 2009).

1.1 Literature Review

The studies regarding competition among species have a very old history. It was in 1934 when Gause gave the competitive exclusion principle stating that species occupying the similar niche could rarely co-exist in the same environment. Twenty two years later Brown and Wilson (1956) came out with the term "ecological character displacement" with the same assumption that the species overlapping with each other significantly can't co-exist. It assumed that when there is an overlap in the geographical ranges of two species their differences are strengthened in the zone of sympatry and falls weaker as we move away from this zone. This hypothesis took under consideration both the 'reproductive character displacement' that must have evolved to shun hybridization and 'ecological character displacement' i.e. the evolution of shape and size difference to minimize resource overlap and inter-specific competition.

The opposite phenomenon was also addressed by Brown and Wilson (1956) which Grant (1972) termed as 'character release'. It says that two closely related species are distinct when occurring together but if one member of the pair occurs alone it converges towards the other in such manner that some of the characters are nearly identical to it. The debate on competitively driven morphological diversification was again put forth by Hutchinson (1959) by asking "why are there so many kinds of animals". With the assumption that the ecologically similar species that are morphologically too same couldn't co-exist, quantitative measures involving morphological shift came to be known as Hutchinson ratios which signified minimal differences between trophic apparati between potential competitors.

Among mammals, there lies a vast literature in the context of character displacement in carnivorans. Undoubtedly it is due to their large geographic ranges and significant morphological differences (Ralls & Harvey 1985; Dayan et al. 1990; VanValkenburgh & Wayne 1994; Simberloff et al. 2000). Ample study has also taken place to understand the preference for different prey size by carnivores of varying body sizes (Gittleman 1985); hence partitioning of resources (Dayan & Simberloff 2005). In Indian sub-continent tiger and leopard are two co-existing large felids. The studies on co-existence of leopards and tigers till date have mostly been conducted in South Asia (Steinmetz 2013). **Below mentioned are the mechanisms and behavior through which sympatric carnivores (with special focus to leopard & tiger) co-exist in nature**:-

(a) Dietary Segregation

Differential patterns of prey selection strategies and availability of ample prey belonging to different size classes make niche segregation, hence the co-existence of leopards and tigers possible in the same landscape (Karanth & Sunquist 1995; Andheria et al. 2007). There is significant dietary overlap between the sympatric tiger, leopard and dhole despite considerable differences in body size (Karanth & Sunquist 1995; Edgaonkar 2008; Ramesh et al. 2009; Selvan et al. 2012; Harihar et al. 2011; Majumder et al. 2013). A study in Nagarahole National Park found that the diet of tiger, leopard and dhole consisted of five ungulate species:sambar (*Rusa unicolor*), barking deer (*Muntiacus muntjak*), wild pig (*Sus scrofa*), gaur (*Bos gaurus*), and chital (*Axis axis*) with a significant overlap of 89-98% (Karanth & Sunquist 1995). All the ungulate species are preyed upon with a variation in frequency of prey preference (see Table 1).

S.No.	Study Site	Intra-guild Species	Large Prey	
			Preferred	Avoided
1.	Nagarhole National Park (Karanth & Sunquist 1995)	Tiger	Gaur (Large Size)	Barking Deer (Small Size)
		Leopard	Chital (In preferred prey weight range and harmless)	Wild Pig (In preferred prey weight range but aggressive)
2.	Bandipur Tiger Reserve (Johnsingh 1983)	Tiger	Sambar (Similar preference of dense habitat in which tiger hunts, lives in small herds, in preferred weight range of tiger	Chital (Behaviour of assembling in open habitats in night making them less prone to predation
		Leopard	-	Wild Pig (same as above)
3.	Bandipur Tiger Reserve (Andheria et al. 2007)	Tiger	Gaur (Large size)	Barking Deer (Small Size)
		Leopard	Chital (same as above)	Sambar and gaur (large size and difficult to handle)

Table 1. Selection of large ungulates by tiger and leopard in various sites in India (with reasons for selection also mentioned).

Primates are also preyed upon by tiger, leopard and dholes but due to the arboreal abilities of leopard these primates form considerable proportion of their diet. (Karanth & Sunquist 1995; Andheria et al. 2007; Wang & Macdonald 2009). Small insectivores and rodents forms a major part of leopard diet when compared to tiger (Sankar & Johnsingh 2002). Karanth & Sunquist (1995) found that in Nagarhole the smaller prey items like Black-Naped Hare (*Lepus nigricollis*) and Indian Porcupine (*Hystrix indica*) are often fed upon by leopard and dhole and not by tiger.

S.No.	Study Site	Intra-guild Species	Prey Species	Preferred sex of the prey	
				Male	Female
1.	Nagarhole National Park (Karanth & Sunquist 1995)	Tiger	Sambar, wild pig & chital	•	-
		Dhole	Chital	•	-
2.	Bandipur Tiger Reserve (Johnsingh 1983)	Dhole	Sambar & chital	•	-
3.	Pench Tiger Reserve (Majumder et al. 2013)	Tiger	Sambar, chital &gaur	•	-
		Leopard	Chital	•	•

Table 2. Preferences of prey gender by tiger, leopard and dhole across the country

Selection on the gender of particular prey species has also been reported. The reason for high predation on males of sambar, gaur and wild pig (see Table 2) by the predators can be attributed to their solitary nature, dispersal behavior and susceptibility to injuries from intra-specific fights. Solitary nature makes them less efficient in detecting the predators when compared to the females who usually live in groups (Schaller 1967; Johnsingh 1983; Karanth & Sunquist 1992). The reason for high predation of male chital was due to their spacing behavior in large herds (Karanth & Sunquist 1995). Leopard in Pench Tiger Reserve was seen predating on both the sexes of chital (Majumder et al. 2013). Studies from Pench Tiger Reserve (Majumder et al. 2013) and Nagarhole National Park (Karanth & Sunquist 1995) have also reported that tiger being larger in size killed more animal in good health when compared to leopards. Such differences were not found in Mudumalai Tiger Reserve (Ramesh et al. 2010).

Preventing Kleiptoparasitism

Leopard: They take carcass on tree to eat and store to prevent kleiptoparsitism from other sympatric carnivores like tiger and dhole as they cannot climb trees. Seidensticker (1976) in Chitwan National Park found that Leopard took half of their kills into trees.

Tiger: Tigers prefer hiding kills in dense cover with the exception of carcasses too heavy to be dragged like gaur kills which are abandoned in the open (Karanth & Sunquist 2000).

(b) Temporal Segregation

Tiger, leopard and dhole may hunt throughout the day but dhole being different from the cats is a diurnal hunter (Johnsingh 1983; Venkataraman et al. 1995; Karanth & Sunquist 2000). In Sariska Tiger Reserve after the tigers got extirpated the leopard was seen most active in the evenings. After Tiger reintroduction in the Sariska leopard's activity period shifted to late evening avoiding the activity period of tiger (i.e. evening). Leopard was found very less active after mid-night which was the peak activity period of tiger. It shows that temporal segregation is a mechanism through which these two ecologically similar species avoids competition. The reason for this temporal variation is the usage of prey resources in different time of the day which promotes co-existence (Karanth & Sunquist 2000). One species makes way for the competitor species and shifts it's time to reduce encounters with it (Mondal et al 2012). However, in Mudumalai Tiger Reserve no active temporal segregation between tiger and leopard was found (Ramesh et al 2012).

Temporal segregation has also been seen in other larger carnivore guild. Jaguar and puma have been known to segregate temporally (Scognamillo et al. 2003; Harmsen et al. 2009). Probably the smaller bodied puma avoids the jaguar (Harmsen et al. 2009). In Africa the guild members have evolved to be active in the period which reduces the likelihood of confronting the dominant lion and that too in limitations of optimal foraging. The subordinate predators are active for a much lower time than their dominant competitors (Hayward & Slotow 2009).

(c) Spatial Segregation

The competition for space could be more intense in the areas which are disturbed and not in the optimal areas (Ramesh et al. 2012). The avoidance of areas with tiger and inhabitation in peripheries of the park near human habitations by leopard has been reported by Seidensticker (1976). In Mudumalai Tiger Reserve, Tiger, Leopard and Dhole were found to be using the same areas (Ramesh et al. 2012).

In Sariska due to tiger reintroduction there was a drastic decline in the leopard population (see Fig. 2). Leopard was seen to avoid areas dominated by tigers and inhabit the one which were seldomly used by them (Mondal et al. 2012). It is the combination of both the prey habitat requirements and the preferences of the prey by the predators which affects the space usage among the competitors. It also varies from season to season. Chital is the principal prey species for dhole and leopard but the areas inhabited by them were avoided by both to reduce inter-specific competition with the larger body sized animal tiger which dominated there (Majumder et al. 2012). It is also the heterogeneity of the habitat which reduces the chances of interaction between tiger and leopard and thereby decreases the effects of dominance (Seidensticker 1976). It was concluded by Sunquist and Sunquist (2002) that leopard co-exists with tiger by avoiding their areas of hunting as well as resting.

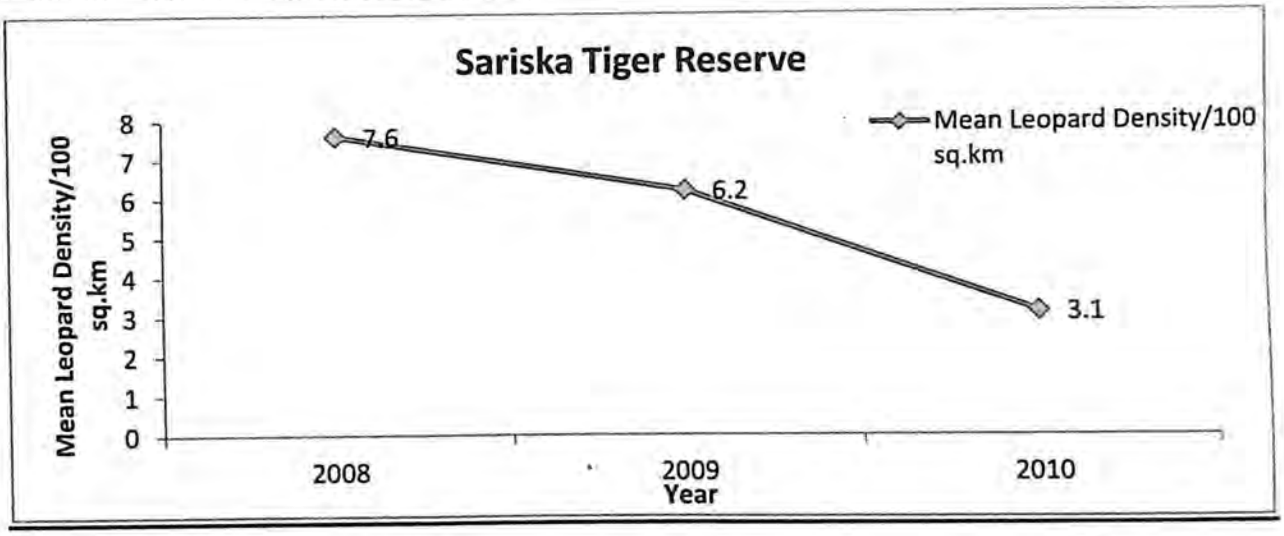


Fig 1. Leopard density prior to Tiger reintroduction in Sariska TR (2008) and its decline after Tiger reintroduction (2009) and the year after reintroduction (2010). Source: Mondal et al. 2012.

In Africa lion is the largest and most dominant predator in guild (Owen Smith and Mills 2008) and occupies the most optimal and resource rich habitats. They are not hesitant to move in the habitat of other carnivores in the guild (Vanak et al. 2013). The subordinate predator reduces the chances of interaction with dominant competitor or predator by avoiding prey rich areas and may inhabit sub-optimal habitats (Chesson 1986; Rosenweig 1991 & Durant 1998). Contrary to this it was also found that the habitat and movement patterns of the sub-ordinate carnivore are in direction of taking risks of fitness cost by utilizing areas occupied by dominant predator rather than avoiding and taking chance of not encountering anything to eat in sub-optimal habitats (Vanak et al. 2013). Jaguar and puma are also known to segregate spatially (Emmons 1987; 1989; Scognamillo et al. 2003). However, recent studies found that jaguar and puma have similar or near similar habitat preferences (Harmsen et al. 2009; Foster et al. 2010).

The top-down effect increases as the resources decline (Polis et al. 1989). However, the apex predators in an ecosystem may be present in such low density that they no longer put forth top-down effects on habitat usage and abundances of meso-predators and the process is termed as meso-predator release. This is now prevalent in many ecosystems due to the drastic loss of top carnivores worldwide (Prugh et al. 2009). The intensity of the release relies on the resource availability for the meso-predators (Elmhagen & Rushton 2007). It has also been perceived that it is not only the density and assemblages of prey that solely allows two species to co-exist and local ecological settings may play a vital role (Harihar et al. 2011). In order to understand the response of communities to such multi-dimensional pressures there is a need for in-depth research in varying ecological set ups (Holt & Polis 1997) along differing gradients of predators and prey (Palomeres & Caro 1999).

1.2. Background of the study

Tiger (*Panthera tigris*) and leopard (*Panthera pardus*) are sympatric in several parts of Asia (Seidensticker 1976). Tigers are four times heavier than leopards (Seidensticker 1976) and it is usually stated that the areas where tigers are abundant leopards are few (Schaller 1967, Johnsingh et al. 2004). Tiger due to its larger body size dominates the leopard (Karanth & Sunquist 1995). Fatal interactions are infrequent in this community (Harihar et al. 2011) but the fear of being killed persuade the animal to avoid habitats and time periods when the larger predator is active (Lima & Dill 1990) and imposes fitness consequences that are commonly as big as those from direct mortality (Preisser et al., 2005; Creel & Christianson 2007; Ritchie and Johnson 2009).

Rajaji National Park (RNP) located in the westernmost part of Terai Arc Landscape (TAL) has been identified as one of the seven "Priorty One" landscapes for tiger conservation in the world. The western sector of RNP is part of one of the nine Tiger Habitat Blocks (THB's) in TAL i.e. THB I whereas, the eastern sector forms the western most limit of THB II which extends further eastwards to Corbett Tiger Reserve through the Lansdowne forest division (Rajaji-Corbett corridor) (Johnsingh & Negi 2003; Johnsingh et al. 2004). RNP is also an integral part of the Rajaji-Corbett Tiger Conservation Unit (RCTCU) which is one of the 11 identified Tiger Conservation Units in Indian sub-continent for long term persistence of tiger (Dinerstein et al. 1997).

Following relocation of human settlements from most of RNP, there has been a tremendous recovery of its habitat. While, the eastern sector of RNP has shown a recovery in the tiger population (Harihar et al. 2009a), tigers are on their way out in the western sector of the park (Harihar et al. 2009b). Over a decade of tiger monitoring in RNP, 42 individual tigers have been documented in the eastern sector of RNP (Bivash Pandav, pers com.). None of these 42 tigers have been photographed in the western sector of RNP. Lack of functional connectivity has been identified as the factor responsible for decline of tiger in western part of RNP (Harihar and Pandav 2012). With the recovery in tiger population in eastern RNP, leopards have shown a declining trend (Harihar et al. 2011). In contrary, with the disappearance of tiger from most of western RNP, leopards are increasingly becoming common in the area (Bivash Pandav, pers com.). Predators play a major role in shaping prey communities. With the tiger being in extremely low densities in western Rajaji (only 2 tigress) leopard is functionally the top carnivore there. Thus, RNP provides a perfect ecological setup to study responses of leopard and prey in varying gradient of tiger densities.

1.3 Study Objectives

Considering the gradient of tiger presence across RNP, the present study was initiated with the following objectives:

I. To assess the abundance of prey in RNP.

II. To determine the abundance and mechanisms of resource partitioning of tiger and leopard in RNP.

Leopard and tiger are sympatric carnivores co-existing in many parts of their distribution range. Tiger being larger in size dominates the leopard. The study aims to answer few key questions about the leopard response in spatial and dietary resource utilization in varying gradient of tiger density in RNP.

1.4 Key Questions

(1) Is there any difference in the densities of major prey species in the tiger occupied and non-tiger occupied habitat?

(2) Is there any difference in the densities of leopard in the tiger occupied and non- tiger occupied habitat?

(3) What is the space use pattern of leopard in tiger occupied and non- tiger occupied habitat?

(4) What is the diet of leopard in the tiger occupied and non- tiger occupied habitat?

Sub-question

(3.1) Is there any dietary overlap among leopard and tiger in eastern RNP?

Sub-question

(3.2) What is the principal and most utilized prey species of leopard and tiger in tiger occupied and non- tiger occupied habitat?

2. Study Area

Rajaji National Park (RNP) is located between 77°57'7" and 78°23'36" East and 29°51'7" N and 30°15'50" North spanning in the Haridwar, Dehradun and Pauri Garhwal districts of Uttarakhand state in Northern India (Uniyal 2006). RNP is spread over an area of 820.42 Km^2 in and around the Shivalik foothills lying in the lesser Himalayas and the upper Gangetic plains. The river Ganga runs through the RNP for about 20 km. and divides it into two parts i.e. western sector of RNP (570 Km^2) and eastern sector of RNP (250 Km^2) (Uniyal et al. 2006). RNP was notified in 1983 by amalgamating three erstwhile wildlife sanctuaries namely Chilla of eastern sector and Motichur and Rajaji from the western sector. The region being part of Shiwalik-Bhabar tract has characters like undulating hills ranging from 400 m to 1200 m with low water table and streams receding into permeable deposits (Harihar et al. 2009b). The southern slopes are much steeper and the streams and seasonal rivers run north to south. The forest type as per Champion and Seth classification (1968) in the region is Northern Indian Moist Deciduous Forest and Northern Tropical Dry Deciduous Forest. The average annual rainfall in this tract is about 1200 mm (Uniyal et al. 2006).

As a whole the land cover matrix is constituted by natural forests interspersed with agricultural and forestry crops. The undisturbed valleys support vast grasslands of *Saccharum spp.* and short grasslands of *Chrysopogon fulvus, Imperata cylindrica*, and *Eragrostis* spp. are found in intensively grazed regions. Key vegetation associations on the south facing slopes are mixed forests comprising tree species such as *Aegle marmelos*, *Anogeissus latifolia*, *Holoptelia integrifolia*, *Lagerstroemia parviflora*, *Ehretia laevis*, *Terminalia alata. Shorea robusta* (sal) dominates forests on the gentle north facing slopes (Harihar et al. 2009b). In total 49 sp. of mammals, 9 species of lizards and 28 species of snakes have been reported from RNP (Uniyal et al. 2006). Tiger and leopard are the two large carnivores found in the area. The major prey species of these large carnivores in the study area are chital *Axis axis*, sambar *Rusa unicolor*, nilgai *Boselaphus tragocamelus*, barking deer *Muntiacus muntjak*, goral *Nemorhaedus goral*, wild pig *Sus scrofa*, terai grey langur *Semnopithecus hector*, porcupine *Hystrix indica*, Indian Peafowl *Pavo cristatus* and hare *Lepus nigricollis.* It is also home to other large mammals like

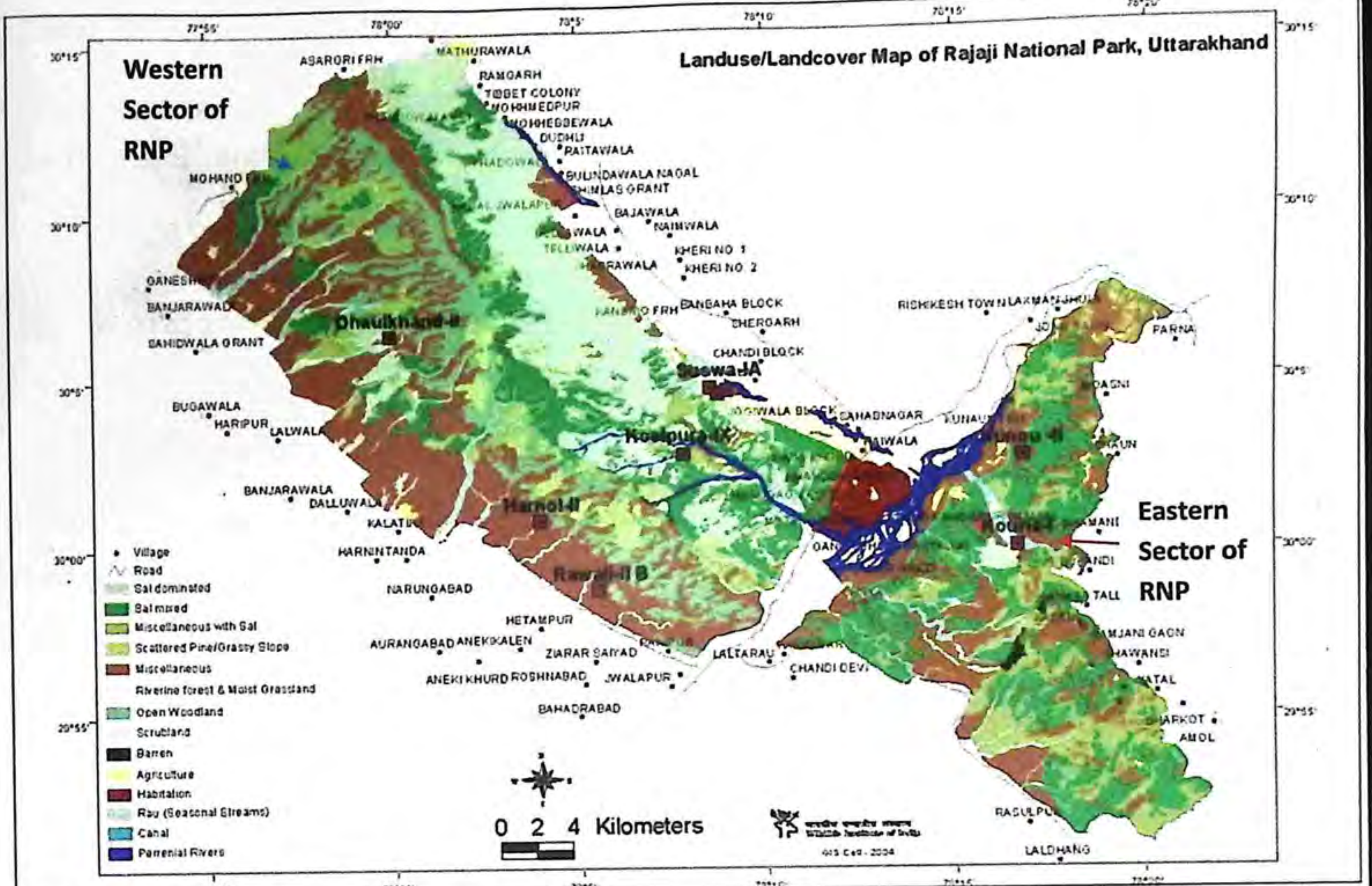


Fig 2. Land use/ Land Cover Map of the intensive study area (Rajaji National Park).

Asiatic elephant *Elephus maximus,* sloth bear *Melursus ursinus,* Asiatic black bear *Ursus thibetanus,* and striped hyena *Hyaena hyaena.* Cattle and buffaloes ranging from the villages on the boundary of the forests are also potential prey species (Harihar et al. 2009). RNP is home to 312 species of birds (Pandey et al. 1994). It is also the north-western most distribution limit of Bengal Tiger, Asiatic Elephant, Great Indian Hornbill and King Cobra (Uniyal et al. 2006).

3. Study Design and Methods

In order to complete the decided objectives the field work (i.e. data collection) was carried out from December 2014 to March 2015. Data analysis was done in month of April-May.

3.1. Estimation of Prey Abundance

3.1.1. Field Method

Estimation of major prey species density was done by the very well known line-transect method (Burnham et al. 1980). 54 permanent transects were laid in the study area of 820.42 Km^2 (Fig. 3). Out of the 54 transects walked, 11 were in eastern sector and 43 in western sector (as much larger than eastern sector). All the representative vegetation types of RNP were kept in the mind while plotting the line transects. The transects were of variable lengths with the smallest being of 0.85 km and the longest being of 2.41 km. Transects were cut in a manner that it just clears the visibility for the observer to detect the animal and not change the habitat or create an open space for ungulates to congregate. The 54 transects were walked at least thrice early in the morning. Evening transects were also walked in the areas which were devoid of human disturbance. The transects were walked from 6.00 AM to 9.00 AM and in evening from 3.00 PM to 5.00 PM as it is the peak activity period of the animals to be active. The activity of ungulates reduces between 9.00 AM to 3.00 PM in the hot period of the afternoons and therefore it is not suggested to walk transect at that time. The 11 transects of eastern sector were replicated temporally at least 7 times and maximum of 8 times. Whereas, out of the 43 transects of western sector 42 were walked

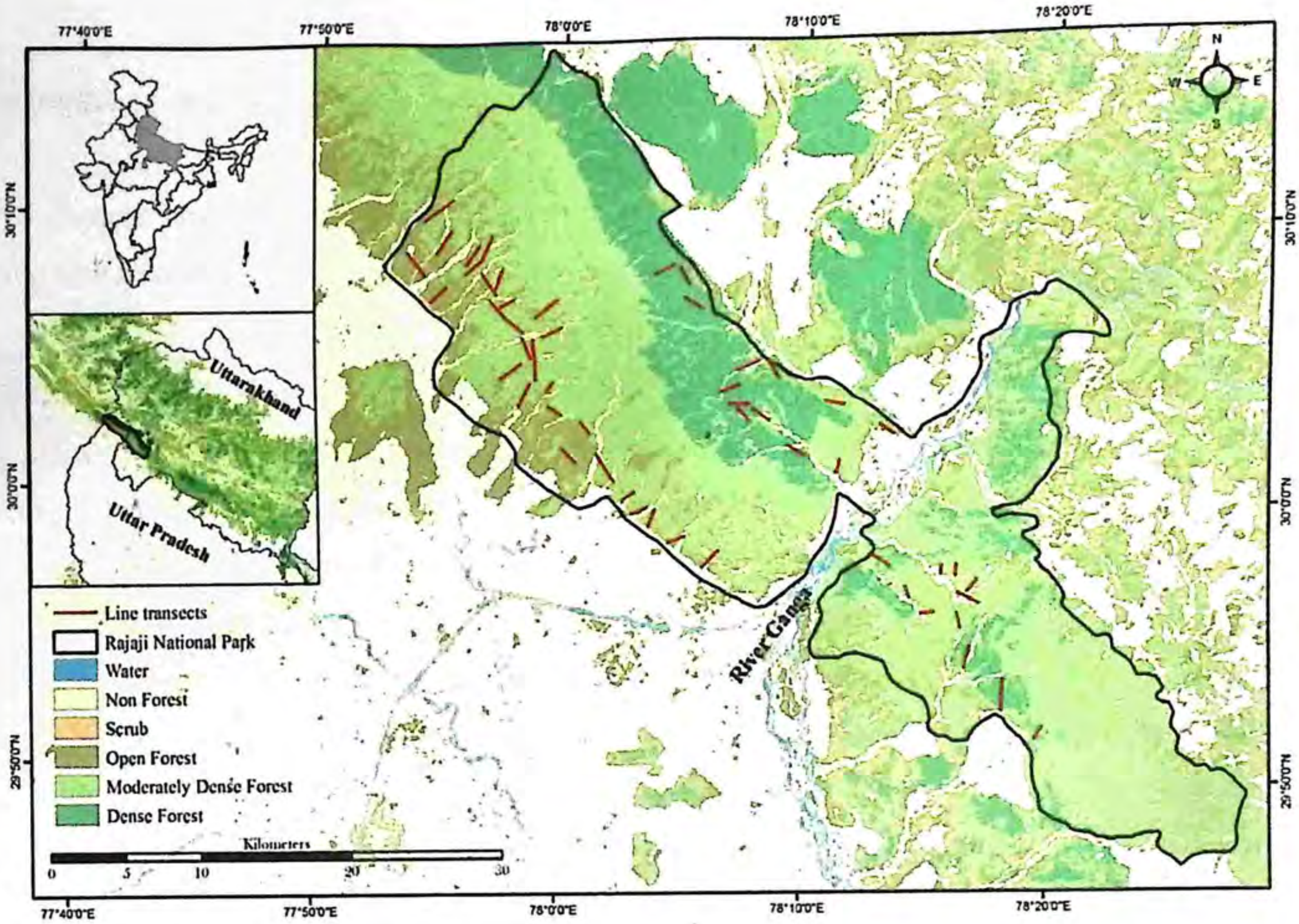


Fig 3. Map showing the lay out of line transects in Rajaji National Park.

minimum thrice and only one transect was walked twice. The total effort of transects in the eastern and western sector of the park is 113.04 km and 237.98 km respectively. The combined effort for all the transects in RNP was 351.02 km.

For each ungulate sighting, following parameters were recorded:

- Date and time of sighting,
- Species ID
- Group size
- Sighting distance
- Animal bearing and walk bearing
- Major Habitat type
- Terrain Type –Flat, undulating and very undulating

• The beginning and ending Global Positioning System (GPS) reading of the transect.

Radial distance was measured using the laser rangefinder (Nikon Laser 1200 S) and the animal bearing was recorded by using SUNTO see through compass.

3.1.2. Analytical Method

Programme Distance 6.2 (Thomas et al. 2010) was used to analyze the data recorded for estimating the density of the major prey species of RNP. The analytical unit used was cluster size of animals as the individual animal information generally underestimates the true variance (Southwell and Weaver 1993). For knowing the distribution of the sighting distances an exploratory analysis was done by clubbing the distances in small intervals and plotting the out coming histograms as recommended by Buckland et al. (2001). On the basis of resultant histograms, the data was truncated for each species at an appropriate distance. The signs of piling, spikes near the line, avoidance movements and steep fall away from the line were investigated. The data was then assembled into appropriate distances for every species so that the detection function gave a good fit. The models like half normal, hazard rate and uniform were fitted with hermite polynomial, simple polynomial and cosine series for every species. The best fit model was the one with the minimum Akaike Information Criterion (AIC) value (Burnham & Anderson 2003).

3.1.3. Estimation of Prey Biomass

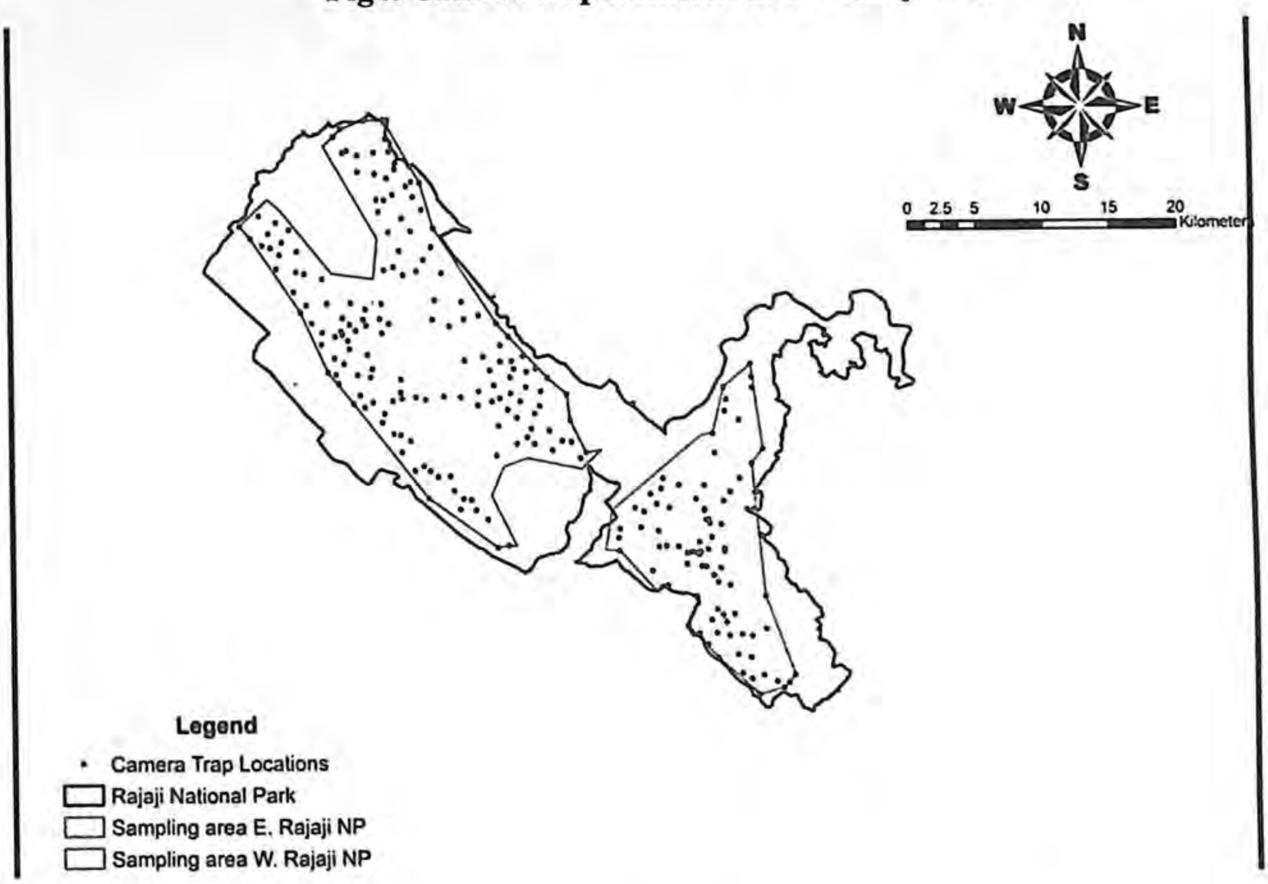
The biomass of prey available in unit area is an ecological value of great importance. The need of documenting the prey biomass has been stated in many studies (Acharya 2007; Karanth and Sunquist 1992; Ramesh 2010). The prey biomass was obtained by multiplying the estimated densities of particular prey and the 3/4th body weight of adult female respectively (Hayward et al. 2006; Hayward et al. 2012). Prey was categorized into small (less than 25 kg), medium (25-150 kg), and large (above 150 kg). The cattle falls in large prey category and its weight was taken from Harihar et al. (2011).

3.2. Estimation of Large Carnivore Abundance

3.2.1. Field Method

Density estimates of tiger and leopard were obtained by using information generated through camera trap pictures on a capture mark recapture framework. Camera trapping was done in all the nine ranges of RNP for estimating the leopard abundances from Dec 2014 till April 2015. The camera-trapping was done block wise due to the logistic reason to sample the whole RNP. It is recommended to place the camera traps intensively in $2km^2$ to $4km^2$ for large carnivores like leopard and tiger for better abundance estimates. Thus, the camera traps were placed in $2km^2$ grid following a reconnaissance in a way to spatially cover the intensive study area. The camera trap sites were selected after exploration to amplify the probability of leopard captures. Panthera and Cuddeback Attack camera traps were used which were placed on both sides of the trail or road in order to get the picture of both flanks of leopard and tiger on all the sites. Trees and wooden posts were used to mount the cameras at a height of 30-40 cms which were then placed 2-3 m away from the centre of the trail or road. Camera traps were kept functional for 24 hours.

Fig4: Camera trap locations in the study area



3.2.2. Analytical Methods

All the photographs of leopard and tiger were sorted out from the larger data set. The photographs which can be clearly identified through the unique rosette or stripe without any ambiguity were selected for individual identification. All the photographs were digitally stamped by date and time of capture. The photographs of camera trap were geo-tagged by location. These images were again segregated into left flank and right flank images. The flank with more number of clear images were used as base to identify unique individuals from unique rosette and stripe patterns and were imported in software named HotSpotter (Crall et al. 2013). HotSpotter is a quick and precise algorithm for identifying animals and has been used for multiple species like lionfish, leopards, giraffe and Grevy's and plains zebra. It identifies unique individuals against a labeled database. It works in two processes (1) extracting and (2) matching key points which are often termed as "hotspots". The first process involves comparing the queried image with the rest in the database and generating a score for the closest possible database image displayed with their respective ranks. Second process involves use of competitive scoring mechanism and matches the image queried with the whole database using a quick nearest neighbor approach. Thus, hotspotter helped in reducing observer error in identifying leopard and tiger due to large amount of dataset and enabled to prepare matrices for spatially explicit capture recapture.

The individuals identified were given unique name ID and were again rechecked manually to clear any kind of chances of misidentification. Further, three researchers having more than 1 year of experience in the field of mark-capture camera-trapping exercise also validated the results by manually identifying the leopards. The leopard pictures which could not be identified were discarded for the analysis. Specific capture and trap matrix were made for tiger and leopard in both the eastern and western sector of the park to make it possible to run in Spatially Explicit Capture Recapture framework (SECR) (Efford 2004; Borchers & Efford 2008).

In SECR, the sampling involves use of detectors in a known spatial framework to sample the unknown distribution of the animals. The detection probability is assumed to decrease with the increase in the distance between the detector and home range centre (Efford 2011).The two parameters involved in this relate to measures of size of home range (σ) and capture susceptibility (g0). The detection process is defined by three parameters i.e. D, g0 and σ. The model fitting is done which includes the both population as well as detection parameters. Unlike the conventional capture-recapture which has N as basic population parameter, SECR has density, D as its basic population parameter. A mathematical function signifies the detection process and explains the declination of animal's detection probability with an increase in distance of detector from animal's home range centre. This detection function has the parameters g0 (intercept) and σ (spatial scale). The estimates of density (D), g0 and σ are obtained by using the model. The population (N) may be derived from this estimates (Efford 2004).

SECR (Efford 2004; Borchers & Efford 2008) yields a much more reliable estimate for the effective trapping area than the conventional closed capture-recapture (Otis et al. 1978) analysis as it utilizes the point of detection of animals to fit a spatial model of the detection process (Efford et al. 2009; Efford et al. 2009). The density obtained by SECR is unbiased by heterogeneous probabilities of capture, incomplete conditions and edge effects and removes the requirement for an ad hoc estimation of the sampling area (Karanth et al. 2006; Soisalo & Cavalcanti 2006; Royle & Young 2006; Royle et al. 2009). SECR analysis was conducted using package 'secr 2.9.4' in R programming environment. The secr package needs only three input files (1) Capture matrix (information on animal identified, trap location and sampling occasion) (2) Trap Matrix (information of spatial locations of traps, dates when particular traps were functional and sampling occasion) (3) Habitat Mask file (i.e. state- space details). In the SECR analysis the area surveyed (i.e. the area covered in network of camera-traps) is combined with a much extended area around it which is known as "habitat mask" or "state space" denoted by S. It is characterized by a large number of regularly placed points which are in the form of very fine lattice. These evenly spaced points are thought to be the potential habitat of the animals in the population being assessed and envisioned as potential home range centers (activity centers) of the animals being captured in the effective trapping area (ETA) (Gopalaswamy et al. 2011).The buffer distance is also given which is large enough to ensure that no animal outside the buffered region has any probability of being captured in camera trap array during the survey and was summed with the rectangle surrounding the trap array. Thus, numbers of regularly spaced points were generated for this summed area using ArcGIS 9.3.

The leopard and tiger density in RNP was estimated by using R programming environment package **secr 2.9.4** (Efford 2015)

The detection function (g0 and sigma) were modeled using parameters as constant (~1), learned response i.e behavior and two group heterogeneity (h2). The following combination of model parameters was used for the analysis.

1. **g0~1 sigma~1** (Null Model) – The model assumes that even after the individuals get camera trapped for the first time there is no change in detection i.e. g_0 and home range measures σ . The probability of capture equals the probability of recapture. g_0 (intercept) and σ (spatial scale).
2. **g0~b, sigma~1** (learned response or Behaviour Model) - There is a change in detection (g_0) after the first capture i.e. behavioral response in capture probability at the home range centre may lead to the avoidance of camera-traps by the animal (trap shyness i.e. common among large carnivores) or attraction towards camera traps (trap happiness, i.e. mostly seen when baits or lure scents are used) but the measures of home range size (σ) remains constant.
3. **g (.) s (b) (Behavior Model)-** The flash of the camera trap may result in such an avoidance of the region that there is a change in home-range size measures after the first capture i.e. behavioral response in capture probability (trap shyness) whereas, there is no change in detection (g_0) and it remains constant.
4. **g (b) s (b) (Behavior model)-** The model assumes that there is a change in detection (g_0) and home range size measures of the population after the first capture (trap happiness or trap shyness).
5. **g_0 s (h_2)** (Heterogeneity model)- This model is group or individual dependent. The capture probability of group differs but the capture is equal to recapture in each group. The two groups in the population has detection constant (g_0) but different measures of home-range.
6. **g (h2) s (.)** (Heterogeneity model) -The model is again group or individual dependent. The capture probability of group differs but the capture is equal to recapture in each group. The two groups in the population have different detections (g_0) but constant home-range measures.
7. **g (h2) s (h2)** (Heterogeneity model)- These model assumes to have two different groups in the population being sampled (which might be categorized into sex, age structure etc.) which

has different detections (g_0) and home range measures. The capture probability of group differs but the capture is equal to recapture in each group here also.

These models were run using half normal detection function as this detection function here make more ecological explanation rather than other detection function as suggested by Efford (2014). These led to a total of 7 models for the double session analysis done for each half normal detection functions for tiger and leopard.

3.3. Dietary and Spatial Niche of Large Carnivores

The food habit of large felids of RNP was assessed in month of April-May 2015. Kill identification, field observation, stomach content analysis and scat analysis are the few of the common methods used to understand large carnivore's diet. Being cost as well as time efficient scat analysis is considered as one of the best and robust method for dietary studies (Schaller 1967, Kruuk 1972, Sunquist 1981, Johnsingh 1983, 1992, Karanth and Sunquist 1995). So, it was decided to use scat analysis method to know the dietary selection and overlap between tiger and leopard diet in RNP.

3.3.1 Food Habits of Large Carnivores

3.3.1(a) Scat collection and laboratory analysis

In the field, scats were collected opportunistically from December 2014 to March 2015 by walking along the trails, forest roads where the large felids like leopard and tiger tend to move (Johnsingh 1983). The presence of field signs like scrape, rakes, sprays and pug-marks etc were used as indicators of major paths used by leopard and tiger for scat collection **(Fig 5.)**

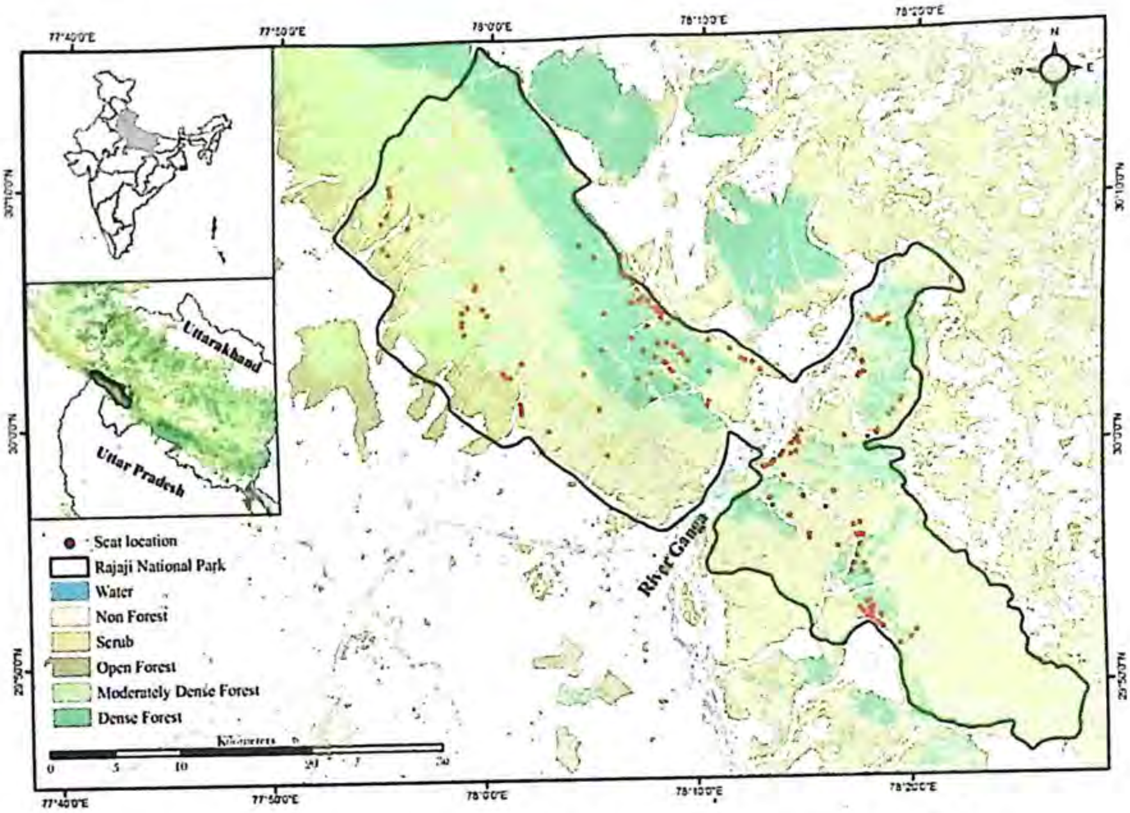


Fig 5. Map showing the points from where scat collected.

The scat of Tiger and leopard were differentiated by some basic field knowledge i.e. size and diameter of the scats. Scat of tiger is less coiled with greater distances between two successive constrictions within a single bolus which in case of leopard has comparatively shorter distances between adjacent constrictions and is much more coiled (Johnsingh 1983). The secondary field signs like pugmarks and scrapes near or around the scats were also taken into the consideration while classifying it into one of the two felids (Johnsingh 1983, Karanth and Sunquist 1995 and Biswas and Sankar 2002). Intensive details like Date, Range, GPS location, place where found, condition of scat (fresh or old), associated carnivore sign and substrate type were also recorded. The unidentifiable scats were rejected there itself in the field to remove and avoid ambiguity.

Scats were brought into the Wildlife Institute of India Laboratory for further analysis. The hair of the prey species remains undigested even after passing through the gut of the carnivore and are one the best entity to identify the consumed species (Ramakrishnan et al. 1999). The hair character like medullary structure (Mukherjee et al. 1994) was the major feature through which microscopic examination of prey hair was done. For identifying the prey species consumed every bolus of the scat was opened up very carefully and ample hair sample were taken in a proportional way from each bolus for randomizing the sampling and leaving no bias. In order to assure the optimal collection of hairs from scat at least 20 hairs were picked up in above mentioned manner for slide preparation. Prior placing the hairs on slides the dirt on the hairs was cleaned with water and then hair were immersed in alcohol to dehydrate. Further, the hairs were cut at both ends and washed with xylene so, that xylene enters the hair and makes the medullary pattern clearly visible through the microscope. The reference slides made by me as well as the ones available in Wildlife Institute of India Laboratory were used to correctly identify the species.

In total 41 tiger scats were analyzed in combination for both eastern and western sector of RNP. Total 168 leopard scats were analyzed of which 74 scats were from eastern RNP and 94 were from western RNP. On dividing the total number of scats having particular prey remains by the total no. of scats with prey remains yielded frequency of occurrence of a particular species (Ackerman et al. 1984). Since, the prey of varying body size are consumed by the predators the frequency of occurrence doesn't actually represent the actual consumed proportion of a species. As an outcome the smaller prey with more hairs per unit body weight gets overrepresented in scats as they produce more scats per unit body weight (Floyd et al. 1978; Ackerman et al. 1984). The scats sometimes have representation of more than one prey species and thus they were given equal weight age for calculating the number of whole scat equivalent for that particular prey (i.e. when two prey sp. consumed 0.5+0.5 and likewise when three prey sp. consumed 0.33+0.33+0.33 respectively). These equi-proportionate values for multiple preys were summed to give whole scat equivalent (collectable scat). On dividing the total number of scats having particular prey remains by the total number of scat with prey remains resulted in the whole scat equivalent (%) of that particular species. The value is in the percentage figure and in particular shows prey intake (Reynolds and Aebischer 1991). The relative biomass consumed of a particular species was also calculated since more than one species occurs quite commonly in a predator's scat (Ackerman et al. 1984, Putman 1984). The dietary studies on large felids have been done using the biomass equation developed by (Ackerman et al. 1984).

3.3.1(b) Biomass equation by Ackerman et al. (1984)

As known very well that in nature prey species of varying sizes is consumed and the digestibility of these varying body-sized animals is different. It makes relative frequency of occurrence unrepresentative of proportion consumed of varying prey species. The smaller prey due to their higher surface to volume ratio has much more hair per unit biomass than the larger prey. So, it leads to production of more scats for smaller prey when compared to larger prey therefore misleading the data by overestimating the consumption of smaller prey in the scats (Floyd et al.1978; Ackerman et al. 1984). To know precise estimation of diet, it became important to correct for this bias and thus feeding trials were used to build up relationships that adjusts the biomass consumed and number of collectable scat produced (Floyd et al. 1978; Ackerman et al. 1984; Jethva and Jhalà 2004). The biomass equations were thus developed which can be used to convert the relative occurrence of prey remains in scat to actual biomass consumed. Ackerman developed a biomass equation with his feeding trials on cougar which has been used by many studies related to large felid diet all round the world (Karanth and Sunquist, 1995, Biswas and Sankar, 2002, Bagchi, et al., 2003, Andheria, et al., 2007). The equation is $Yi = 1.98 + 0.035\ X$, where Xi represents the live weight of the prey species i and Yi is the weight of prey in one collectable scat Y (Ackerman et al. 1984).

3.3.1(c) Shortcomings of biomass equation developed by Ackerman et al. (1984)

The development of the biomass equations has been through the feeding trials carried out on temperate species and has been largely used for large carnivore diet studies in Indian sub-continent. The application of this equation to the tropical system is limited (Jethva and Jhala 2004). It is due to the difference in the surface area to body mass ratio and coat characters between temperate and tropical prey species. These features change the digestibility of tropical prey species from temperate species (Jethva and Jhala 2004). The other reason which creates errors in the diet related studies of large felids is that cougar vary greatly in the body size from much larger lion and tiger and its prey size range is also different. Thus, the range of prey weight presented to cougar in feeding trials by Ackerman et al. (1984) may not be appropriate for representing the suitable prey range of tiger and lion. Thus, the use of Ackerman et al. (1984) may lead to biased results in dietary studies of tropical felids.

3.3.1(d) Biomass equation by Chakrabarti et al. (2013) for tropical felids

Keeping in mind the shortcomings of Ackerman et al. (1984) the new biomass equation for tropical felids was developed by conducting trials on carnivores of all sizes like leopard, lion and jungle cat by providing them the prey of all weight ranges. The new equation came with the conclusion that the Ackerman's equation (1984) overestimated the large prey consumption thereby underestimating the medium sized prey like spotted deer etc. in diet of large felids like tiger, lion and leopard (Chakrabarti et al. 2013). The biomass equations were developed for lion, leopard and jungle cat and a generalized equation for tropical felids was also developed. The Ackerman's equation showed a linear relationship between the biomass consumed per collectable scat (i.e. the biomass taken to produce one collectable scat increased linearly with the body weight of prey species). But, the picture is different as per Chakrabarti et al. (2013) as the biomass consumed to produce one collectable scat increases linearly with the body weight initially but reaches a satiation point after certain body weight where there is no effect of prey weight on the biomass consumed per collectable scat which makes more ecological sense.

For this particular study the biomass equation developed for leopard was used to know the food habits of leopard in RNP and the generalized equation was used to know the diet of tiger in RNP. The generalized equation for tropical felids (used in this study for tiger) and equation for leopard are mentioned here as under:-

Generalized Equation for Tropical Felids (Tiger)

$Y_g = 0.029 \cdot (1-e^{-9.909X_g})$

where Y_g = biomass consumed to produce one collectable scat scaled to predator body mass

X_g = mean prey weight per predator mass

Biomass Equation for Leopard

$Y = 1.922(1-e^{-0.123X})$

where Y= Biomass Consumed per collectable scat, X= Prey Weight

The below mentioned things were looked into to know the diet of large carnivores in RNP.

3.3.1 (e) Principal Prey of Large Carnivores in RNP.

The principal prey is the one which contributes most to a predator's diet. The prey which has highest contribution of relative biomass consumed in a predator's diet is the principal prey. As tiger is larger of the two sympatric carnivores and is the more dominant over leopard (Karanth & Sunquist 1995) it was believed that tiger's prey selection won't change in either of the two sectors. So, to get a representation of larger sample size the tiger scats of western as well as eastern sector were merged to look into the prey selection and dietary niche overlap of leopard and tiger in the eastern sector of RNP.

The prey species were divided into three categories based on their body weight which have been mentioned here as under:-

(1) Large Prey- (weighing from 150 kg or above)
(2) Medium sized Prey- (weighing from 25 to 150 kg)
(3) Small Sized Prey- (weighing less than 25 kg)

For the present study biomass equation developed by Chakrabarti et al. (2013) were used to understand the diet patterns of tiger and leopard in RNP.

3.3.1 (f) Prey Selection of large carnivores in RNP

The term prey selectivity can be defined as hunting a prey species at frequencies differing from what is available (Chesson 1978). If no prey selectivity takes place in carnivores than they should consume a prey in relative frequencies similar to that of its availability in the nature. Looking at the ratio of how much proportion is contributed by a prey in predator's diet and how much is available in nature, it becomes evident that which prey is being more utilized and which is being less utilized. To depict prey selection of large carnivores, the Ivlev's Index (PI) (Ivlev 1961) was used:

$$PI = \frac{(U - A)}{(U + A)}$$

Where U = utilized biomass of prey, A = available biomass of prey.

Prey selection was estimated by the relative biomass consumed values extracted from Chakrabarti et al. (2013).

3.3.1 (g) Dietary Overlap

Dietary overlap among the tiger and leopard in RNP was found by using Pianka's Index of niche overlap (Pianka 1973) in Ecosim 7.0 (Gotelli & Entsminger 2001). The index scales from 0 to 1 and the similarity in niche becomes stronger when the value is closer to 1. The below given formula yields pianka's index of niche overlap, where pi is proportion of prey species i in the diet of tiger (p_1) and leopard (p_2).

$$O_{12} = O_{21} = \frac{\sum_{i-1}^{n} p_{2i} p_{1i}}{\sqrt{\sum_{i-1}^{n} \left(p_{2i}^{2}\right)\left(p_{1i}^{2}\right)}}$$

3.3.2. Spatial Separation between Tiger & Leopard in RNP

The contours associated with the home range centre of each detected individual essentially represent two dimensional confidence intervals for its home range centre, given the fitted observation model. Summing these gives a summed probability density surface for the centers of the observed individuals and to this we can add an equivalent scaled probability density surface for the individuals which were not captured. The fx.total argument of secr 2.9.3 (Efford 2014) was used to generate the spatial realization of density surface in the area of minimum bounding polygon of traps with a buffer of one kilometer. The density surface was not generated for overall model fitted mask area, as I did not have information outside the trapping area. The selection of one kilometer buffer around the minimum trapping polygon was justified on the basis of the probability contour of home range centre of detected animal and equivalently scaled probability of non-captured individuals.

4. Results

4.1. Estimation of Prey Abundance

I estimated prey abundance in eastern and western part of RNP through distance sampling on line transects with an effort of 113.04 km and 237.98 km walk respectively. Field data from line transect were recorded for seven prey species (chital (*Axis axis*) ; sambar (*Rusa unicolor*) ; primates (*Macaca mulatta and Semnopithecus hector*); Red Jungle fowl (*Gallus gallus*), wild pig (*Sus scrofa*) ; Indian Peafowl (*Pavo cristatus*) and nilgai (*Boselaphus tragocamelus*).Although barking deer (*Muntiacus muntjac*) and Goral (*Naemorhaedus goral*) were also sighted on the transects but their observations were too low to get any ecological inferences and thus they were not considered while doing analysis. To estimate overall prey density in eastern and western part of RNP, numbers of detection of each species are shown in (Table 3, 4) below.

The line transect surveys yielded more than 20 visual detections for chital and sambar enabling us to fit detection functions reasonably well and generate density estimates. (Table 3). The number of detections for wild pigs (n =12) , red jungle fowl (n =13), peafowl (n =10) , nilgai (n =3), primate (n =22) were inadequate for reliable density estimation (Buckland et al. 2001). Therefore, we borrowed density estimates derived from a larger set of 43 transects from western RNP, and assumed detection probabilities to be uniform across the wider area (Table 4). However, chital and sambar were abundant in the study area as indicated by encounter rate of species (Table 3) and potentially the most important prey for tiger and leopard because of their biomass and availability.

The results of the DISTANCE 6.2 (Thomas et al. 2010) analysis are presented in Table.3, 4 showing the number of detections, estimated density of clusters, estimated cluster size (mean cluster size where there was no size bias in detection), and mean density of individuals, percent coefficient of variation. Based on the criterion of lowest AIC, the hazard rate key function fit all the prey species data with simple polynomial adjustment terms.

Among Ungulates, Chital was found to be the most abundant ungulate species in eastern and western part of RNP. The density estimate for chital was 23.61±9.21 /sq km in eastern and 21.77±4.32 /sq km in western RNP (Table 3, Figure 4). Sambar was found to be higher in western RNP with density estimate of 15.65±2.52 /sq km in comparison to eastern (10.61±3.21 /sq.km) while wild pig occurred with a density of 8.22±6.95 /sq km in eastern and 5.10±1.87 / sq.km. in western rajaji (Table3). Nilgai showed very low density (0.70±0.81 and 1.91±1.02) in both the eastern and western part of RNP respectively. Among other prey species, Primates are abundant prey species in both eastern (12.92±5.63) and western RNP (11.93±3.90) followed by Red jungle fowl (11.40±8.07) and peafowl (10.28±2.82) respectively.

Site	Species	Best Model	Chi square px2	No. of observations (n)	Effective strip width (ESW)	Encounter rate (n/l)	Detection probability $\hat{P}$ [SE]	Cluster size Density $D\hat{S}$ [SE]	Mean Cluster size E(S) [SE]	Density $\hat{D}$ [SE]
Eastern RNP	Chital	Hazard Rate-Simple Polynomial	0.958	71	36.36 [7.32]	0.62 [0.19]	0.15 [0.03]	8.63 [3.21]	2.73 [0.32]	23.61 [9.21]
	Sambar	Hazard Rate-Simple Polynomial	0.963	57	38.50 [6.33]	0.50 [0.12]	0.32 [0.05]	6.54 [1.92]	1.62 [0.12]	10.61 [3.21]
Western RNP	Chital	Hazard Rate-Simple Polynomial	0.808	139	46.70 [4.44]	0.58 [0.09]	0.11 [0.01]	6.25 [1.13]	3.48 [0.27]	21.77 [4.32]
	Sambar	Hazard Rate-Simple Polynomial	0.818	116	26.02 [2.62]	0.48[0.05]	0.15 [0.01]	9.36 [1.38]	1.67 [0.10]	15.65 [2.52]

Table 3. Density of major prey in the Eastern RNP and Western RNP in 2015

Site	Species	Best model	Chi square p value	No of observations(n)	Effective strip width (ESW)	Encounter rate(n/l)	Detection probability $\hat{P}$ [SE]	Cluster size Density $D\hat{S}$ [SE]	Mean Cluster size E(S) [SE]	Density $\hat{D}$ [SE]
Eastern Rajaji	Wild Pig	Hazard Rate-Simple Polynomial	0.85498	12	19.35 [3.86]	0.10 [0.08]	0.07[0.01]	2.74 [2.26]	3.00 [0.56]	8.22 [6.95]
Western Rajaji				23		0.96[0.02]		2.49 [0.85]	2.04 [0.26]	5.10 [1.87]
Eastern Rajaji	Nilgai	Hazard Rate-Simple Polynomial	0.89625	3	99.78 [25.56]	0.26 [0.24]	0.18 [0.04]	0.13 [0.12]	5.33 [3.38]	0.70 [0.81]
Western Rajaji				28		0.11 [0.05]		0.58 [0.30]	3.25 [0.52]	1.91 [1.02]
Eastern Rajaji	Red Jungle Fowl	Hazard Rate-Simple Polynomial	0.80049	13	15.12 [2.06]	0.11 [0.07]	0.14 [0.02]	3.80 [2.51]	3.00 [0.75]	11.40 [8.07]
Western Rajaji				53		0.22 [0.04]		7.36 [1.92]	1.39 [0.11]	10.28 [2.82]
Eastern Rajaji	Indian Peafowl	Hazard Rate-Simple Polynomial	0.43992	10	28.89 [5.42]	0.08 [0.05]	0.13 [0.02]	1.53 [0.94]	2.10 [0.37]	3.21 [2.06]
Western Rajaji				48		0.20 [0.08]		3.48 [1.53]	2.18 [0.26]	7.63 [3.49]
Eastern Rajaji	Primate	Hazard Rate-Simple Polynomial	0.60054	22	42.79 [7.18]	0.19 [0.06]	0.15 [0.02]	2.27 [0.90]	5.68 [1.03]	12.92 [5.63]
				38		0.15[0.03]		1.86 [0.48]	6.39 [1.25]	11.93 [3.90]

Table 4. Density of other prey species in the Eastern RNP and Western RNP in 2015.

4.1.1 Estimating Prey Biomass

The prey biomass was calculated for both the sectors of the park i.e. eastern and western sector. The prey biomass of ungulates in eastern sector came out to be **3334.94 kg km-^{2}** (Table 5) whereas; the total biomass available in the eastern sector of the park along with smaller prey was **3428.51 kg km-^{2}** (Table 5). On the other hand the ungulate prey biomass in the western sector of the park was comparatively higher i.e. **4345.59 kg km-^{2}** (Table 5) and total prey biomass came up to be **4455.32 kg km-^{2}** (Table 5).

S. No.	Site	Prey	Body Wt. (kg.)	Density (km^{-2}) (S.E)	Biomass (kg km^{-2})
1.	Eastern RNP	Chital	30	23.61 [9.21]	708.3
		Sambar	200	10.61[3.21]	2122
		Wild Pig	47	8.22 [6.95]	386.34
		Nilgai	169	0.70 [0.81]	118.3
		All Ungulates		**43.14 km-2**	**3334.94 kg km-2**
		Primates	6	12.92 [5.63]	77.52
		Indian Peafowl	5	3.21 [2.06]	16.05
		Red Jungle Fowl		11.40 [8.07]	
		TOTAL		**70.67 km-2**	**3428.51 kg km-2**
2.	Western RNP	Chital	30	21.77 [4.32]	653.1
		Sambar	200	15.65 [2.52]	3130
		Wild Pig	47	5.10 [1.87]	239.7
		Nilgai	169	1.91 [1.02]	322.79
		All Ungulates		**44.43**	**4345.59 kg km-2**
		Primate	6	11.93 [3.90]	71.58
		Indian Peafowl	5	7.63 [3.49]	38.15
		Red Jungle Fowl		10.28 [2.82]	
		TOTAL		**74.27 km-2**	**4455.32 kg km-2**

Table 5. Biomass availability of ungulates and total prey in Eastern RNP and Western RNP.

4.2. Estimation of Large Carnivore Abundance

The total number of trap nights during the whole camera trapping exercise was 5582 out of which 1664 were in the eastern sector and 3918 in the western sector. The numbers of detectors used in eastern and western sector of the park were 83 and 164 respectively. The total number of tiger images captured in whole RNP was 177. Out of which 116 were from eastern sector and 61 from western sector. Total leopard images captured in whole RNP was 1536. The number of images photographed in eastern and western sector of the park was 293 and 1243 respectively. Mt+1for leopard in eastern RNP and western RNP was 58 and 109 respectively. As a whole 167 unique individual leopards were identified from the camera trap images from entire RNP.

4.2.1. Density estimate of Leopard

The model g0 ~1σ~h2 (heterogeneity) was ranked as the most appropriate model for leopard density estimates based on its minimum AIC. Since 40 % of the leopards of the eastern sector were not recaptured and to get precise estimates the detection function parameters were borrowed from western RNP by doing multi-session analysis. Each session was regarded as a sampling area i.e. eastern RNP and western RNP. The detection functions were kept common for both the sessions. For the model g0 ~1σ~h2 the density estimates of leopard was 29.01± 4.00/100 sq.km and 25.37 ± 2.63/100 sq.km for the eastern and western sector respectively. The best three models bases on their AIC values are mentioned below in the (Table 6) along with the associated details:-

Sl. No.	Detection Function	Model	AIC	ΔAIC	Trap Nights	Mt+1	Pop. Mixture (p-mix)	σ (S.E) in kms.	g0 (S.E)	pmix1: pmix2	Density/100 km² (S.E)	Site
1	Half Normal	g0 ~1σ~h2	2801	0	1664	58	pmix 1	1.88 (0.08)	0.10 (0.0069)	0.14:0.85	29.01 (4.00)	Eastern RNP
							pmix 2	0.73 (0.03)	0.10 (0.0069)			
					3918	109	pmix 1	1.88 (0.08)	0.10 (0.0069)		25.37 (2.63)	Western RNP
							pmix 2	0.73 (0.03)	0.10 (0.0069)			
2	Half Normal	g0 ~h2 σ~1	2981	180	1664	58	pmix 1	1.15 (0.02)	0.16 (0.018)	0.29:0.70	28.41 (3.83)	Eastern RNP
							pmix 2	1.15 (0.02)	0.03 (0.0054)			
					3918	109	pmix 1	1.15 (0.02)	0.16 (0.018)		24.68 (2.45)	Western RNP
							pmix 2	1.15 (0.02)	0.03 (0.0054)			
3	Half Normal	g0 ~1 σ ~1	3085	284	1664	58	-	1.13 (0.02)	0.08 (0.005)	-	26.07 (3.45)	Eastern RNP
					3918	109		1.13 (0.02)	0.08 (0.005)		22.84 (2.21)	Western RNP

Table 6. Best three models with their minimum AIC and corresponding leopard densities in Eastern and Western Sector of Rajaji National Park

4.2.2. Density estimate of Tiger

The model g0 ~1 σ ~1 (null) was ranked as the most appropriate model for estimating tiger density based on its minimum AIC. The sample size was very small and thus to get precise estimates the detection function parameters were borrowed from the two tigresses of western RNP by doing multi-session analysis. Each session was regarded as a sampling area i.e. eastern RNP and western RNP. The detection functions were kept common for both the sessions. The heterogeneity models g0 ~1σ~h2 and g0 ~h2σ~h2 failed as heterogeneity models are data hungry. For the model g0 ~1σ~1 the density estimates of tiger was 3.03±0.95 /100 sq.km and 0.28 ±0.23 /100 sq.km (since only two tigresses left in western sector) for the eastern and western sector respectively. The best two models bases on their AIC values are mentioned below in the (Table 7) along with the associated details:-

.No.	Detection Function	Model	AIC	ΔAIC	Trap Nights	Mt+1	Pop. Mix. (p-mix)	σ (S.E) in kms.	g0 (S.E)	pmix1: pmix2	Density/ 100 km2 (S.E)	Site
1	Half Normal	g0 ~1 σ ~1	508	12	1664	11	-	2.70 (0.22)	0.04 (0.005)	-	**3.03 (0.95)**	Eastern RNP
					3918	2					**0.28 (0.23)**	Western RNP
2	Half Normal	g0 ~h2 σ~1	512	16	1664	11	pmix 1	2.70 (0.22)	0.04 (0.03)	0.13:0.86	**3.02 (0.95)**	Eastern RNP
							pmix 2	2.70 (0.22)	0.04 (0.007)			
					3918	2	pmix 1	2.70 (0.22)	0.04 (0.03)		**0.28 (0.23)**	Western RNP
							pmix 2	2.70 (0.22)	0.04 (0.007)			

Table 7. Best two models with their minimum AIC and corresponding tiger densities in Eastern and Western Sector of Rajaji National Park.

The (Fig. 6) shows considerable difference in the density of tigers in eastern and western sector of the park but there is no significant difference in the densities of leopard in the eastern and western sector of the park. The density of leopard is higher in the eastern sector than the western sector of the park.

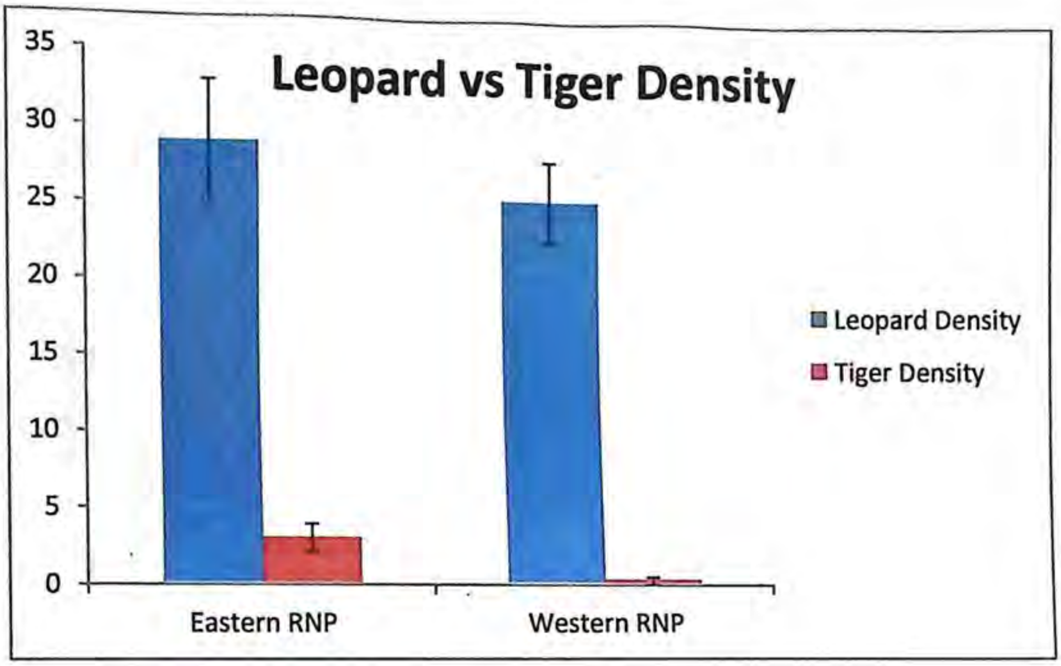


Fig. 6 Leopard vs. Tiger density in the eastern and western sector of RNP

4.3. Prey Selection and Food Habits of Large Carnivores

The principal prey is the one which relatively contributes most to a predator's diet. The prey species were divided into three categories based on their body weight which have been mentioned here as under:-

- Large Prey- (weighing from 150 kg or above)
- Medium sized Prey- (weighing from 25 to 150 kg)
- Small Sized Prey- (weighing less than 25 kg)

The principal prey of tiger and leopard was derived by the relative biomass consumed through Chakrabarti et al. (2013). The equation developed for tropical felids by Chakrabarti et al. (2013) gives much more insight into the feeding ecology of leopard and tiger. The resultant principal preys of leopard and tiger are given as under:-

4.3.1. Principal Prey of Leopard

	Prey	No.	%	Site
Leopard (*Panthera pardus*) (n=74)	Chital (*Axis axis*)	38	38.38	Eastern RNP
	Sambar (*Rusa unicolor*)	23	23.23	
	Cattle	5	5.05	
	Nilgai (*Boselaphus tragocamelus*)	2	2.02	
	Wild Pig (*Sus scrofa*)	1	1.01	
	Primate [Terai Grey Langur (*Semnopithecus hector*),Rhesus Macaque (*Macaca mulatta*)]	11	11.11	
	Rodent	18	18.18	
	Bird	1	1.01	

Table 8. Number of prey items and proportion (%) of different prey species in leopard diet as derived from scat data from Eastern RNP.

Predator	Prey	X (kg)	A (%)	*Y(kg/scat)	*D (%)	Site
Leopard	Chital	30	51.35	1.87	51.02	Eastern RNP
	Sambar	200	31.08	1.92	29.33	
	Cattle	175	6.75	1.92	7.76	
	Nilgai	169	2.70	1.92	2.58	
	Wild Pig	47	1.35	1.91	1.72	
	Primate	6	14.86	1.00	6.15	
	Rodent	0.5	24.32	0.11	1.21	
	Bird	1	1.35	0.22	0.19	

Table 9. Frequency of occurrence (A), relative biomass consumed (D) by leopard based on 74 scats.

***Y (kg/scat) and D (%) calculated by using Chakrabarti et al. (2013).**

	Prey	No.	%	Site
Leopard (*Panthera pardus*) (n=94)	**Chital (*Axis axis*)**	43	35.53	**Western RNP**
	Sambar (*Rusa unicolor*)	42	34.71	
	Cattle	2	1.65	
	Nilgai (*Boselaphus tragocamelus*)	8	6.61	
	Wild Pig (*Sus scrofa*)	2	1.65	
	Primate [Langur (*Semnopithecus hector*), Rhesus Macaque (*Macaca mulatta*)]	8	6.61	
	Rodent	13	10.74	
	Bird	1	0.82	
	Porcupine (*Hystrix indica*)	2	1.65	

Table 10. Number of prey items and proportion (%) of different prey species in leopard diet as derived from scat data from Western RNP

Predator	Prey	X (kg)	A (%)	*Y(kg/scat)	*D (%)	Site
Leopard	Chital	30	45.74	1.87	39.04	Western RNP
	Sambar	200	44.68	1.92	44.90	
	Cattle	175	2.12	1.92	2.46	
	Nilgai	169	8.51	1.92	7.39	
	Wild Pig	47	2.12	1.91	1.22	
	Primate	6	8.51	1.00	3.21	
	Rodent	0.5	13.82	0.11	0.66	
	Bird	1	1.06	0.22	0.14	
	Porcupine	10	2.12	1.36	0.87	

Table 11. Frequency of occurrence (A), relative biomass consumed (D) by leopard based on 94 scats.

***Y (kg/scat) and D (%) calculated by using Chakrabarti et al. (2013).**

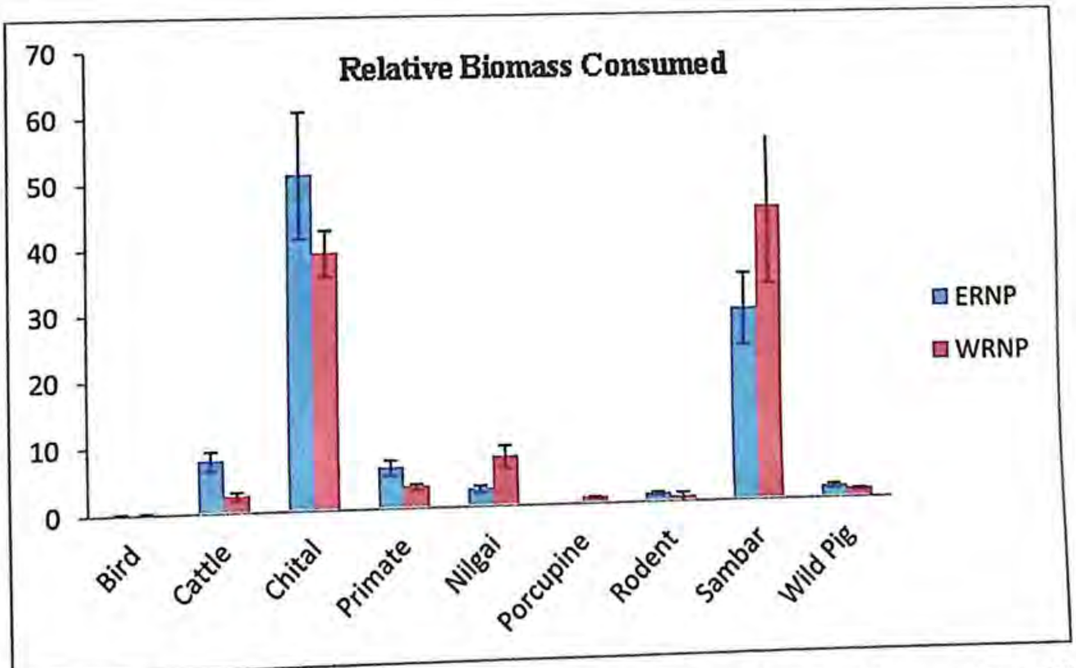


Fig. 7 Bar graph showing the principal prey of leopard in eastern RNP and western RNP

Principal Prey of Leopard in ERNP - Chital is the principal prey of leopard and constituted 51.02 % of leopard diet. Sambar on the second place formed 29.33% of leopard's diet. On the whole the large prey formed 39.67% of leopard's diet whereas the medium sized prey contributes 52.74% to leopard. Small sized prey forms only 7.55% of leopard diet (see Table 9).

Principal Prey of Leopard in WRNP - Sambar is the principal prey of leopard forming 44.90% of total biomass consumed. Chital on the second formed 39.04% part of leopard's diet. Larger body sized prey formed 54.75% of total biomass consumed. Medium body sized prey formed 40.26% and small body sized animals formed 4.88% of total biomass consumed (see table 11).

4.3.2. Principal Prey of Tiger

	Prey	No.	%	Site
Tiger (n=41)	Chital (*Axis axis*)	22	43.13	Whole RNP
	Sambar (*Rusa unicolor*)	17	33.33	
	Cattle	3	5.88	
	Nilgai (*Boselaphus tragocamelus*)	4	7.84	
	Primate [Langur (*Semnopithecus hector*),Rhesus Macaque (*Macaca mulatta*)]	2	3.92	
	Rodent	3	15.88	

Table 12. Number of prey items and proportion (%) of different prey species in tiger diet (percent occurrence) as derived from scat data from Rajaji National Park.

Predator	Prey	X (kg)	A (%)	*Y(kg/scat)	*D (%)	Site
Tiger	Chital	30	51.35	3.75	43.23	Whole RNP
	Sambar	200	31.08	4.34	41.70	
	Cattle	175	6.75	4.34	7.03	
	Nilgai	169	2.70	4.34	7.03	
	Primate	6	14.86	1.42	0.76	
	Rodent	0.5	24.32	0.14	0.22	

Table 13. Frequency of occurrence (A), relative biomass consumed (D) by tiger based on 41 scats.

***Y (kg/scat) and D (%) calculated by using Chakrabarti et al. (2013).**

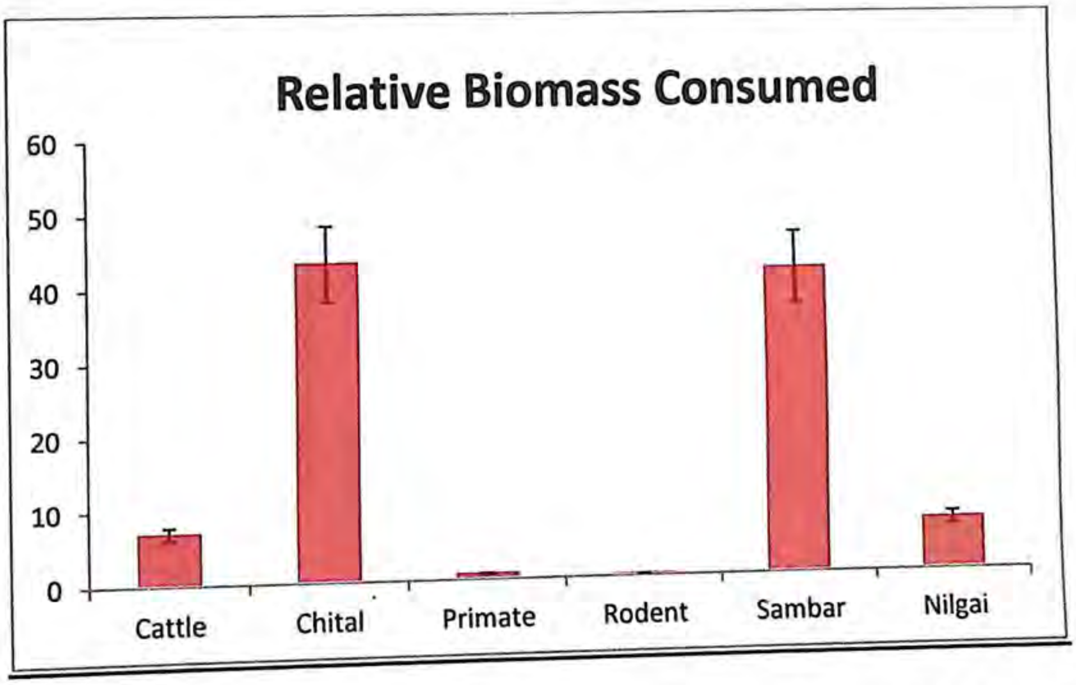


Fig. 8. Bar graph showing the principal prey of tiger in RNP.

Principal Prey of Tiger - Chital is the principal prey of tiger forming 43.23% of total biomass consumed. Sambar being almost equivalent constituted 41.70% part of tiger's diet. Larger body sized prey formed 55.76% of total biomass consumed. Chital was the only medium-sized consumed and small body sized animals formed negligible proportion of total biomass consumed i.e. 0.98% (Table 13).

4.3.3 Prey Selection by Tiger and Leopard in Rajaji National Park

Prey selection in RNP was estimated by Ivlev's Index (Ivlev 1961). Prey selection was estimated through Ivlev Index and chi square statistics was used to compare use versus availability with the help of Scatman (Hines 2002).

$$PI = \frac{(U - A)}{(U + A)}$$

Where U = utilized biomass of prey (x) and A = available biomass of prey (x).

4.3.3 (a) Prey Selection of leopard in Eastern RNP & Western RNP

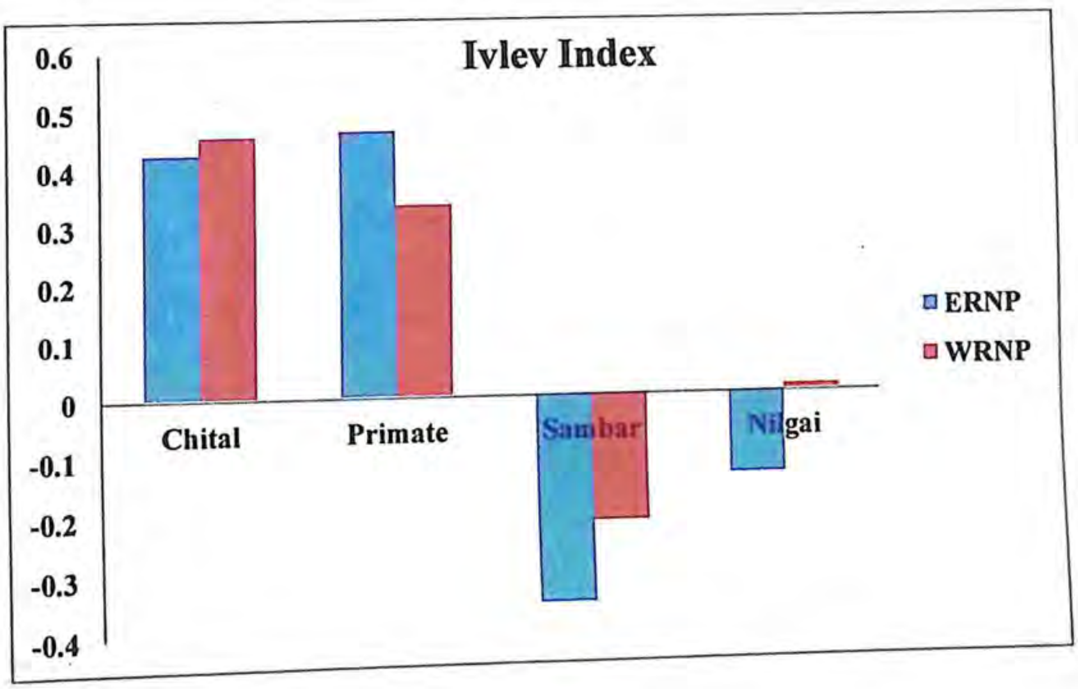


Fig. 9. Prey selection of leopard in eastern RNP and western RNP

Species	Observed	Estimated Expected	Chi-squared	p-value	Standard Error
Chital	30.33	11.75	37.063	0	0
Sambar	17	34.32	22.1824	0	0
Nilgai	1.5	1.91	0.0925	0.761	0.0013
Primate	6.83	2.4	8.5207	0.004	0

Table 14. Chi square statistics comparing use versus availability of leopard prey in Eastern RNP.

Species	Observed	Estimated Expected	Chi-squared	p-value	Standard Error
Chital	32.5	12.06	40.7279	0	0
Sambar	36.5	56.34	22.9415	0	0
Nilgai	6	5.81	0.0067	0.935	0.001
Primate	5	2.47	2.6777	0.102	0.0003

Table 15. Chi square statistics comparing use versus availability of leopard prey in Western RNP.

The Ivlev's prey selection index gave the following values for prey selection by leopard in eastern RNP and western RNP (Fig. 9). Chital and Primate are most utilized prey of leopard in eastern RNP and western RNP. Nilgai is marginally positively utilized in western sector but under utilized in eastern sector. Sambar is not utilized as per its availability in both the sector of the park.

4.3.3 (b) Prey Selection of Tiger in Rajaji National Park

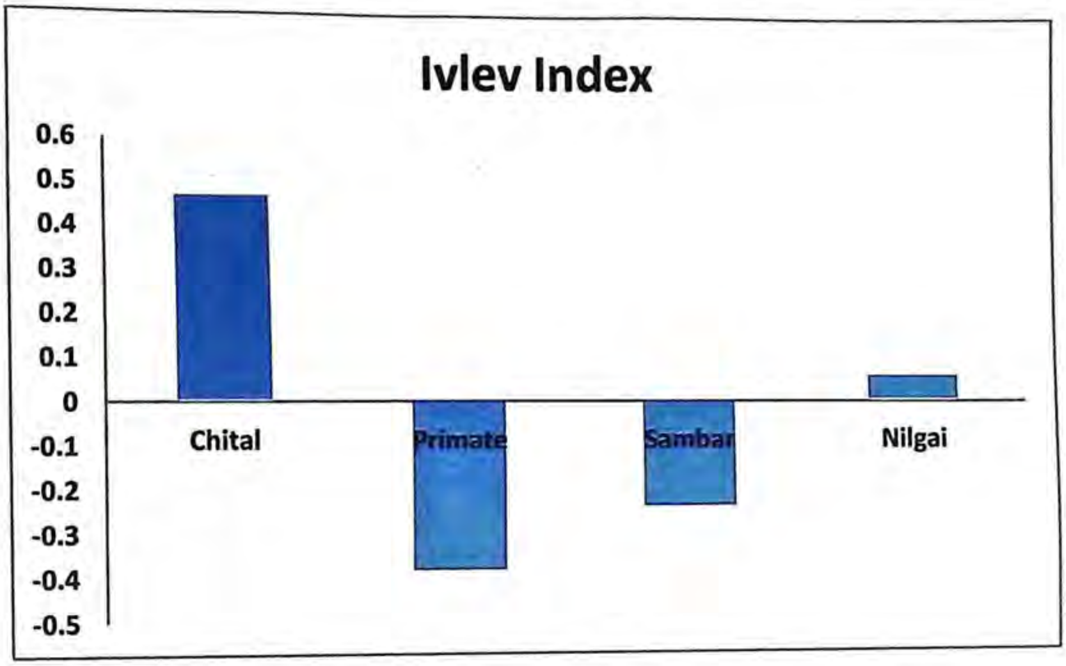


Fig 10. Prey selection of tiger in Rajaji National Park

Species	Observed	Estimated Expected	Chi squared	p-value	Standard Error
Chital	17.83	6.14	26.8195	0.000	0
Sambar	14.83	26.18	18.0543	0.000	0
Nilgai	2.5	2.4	0.0041	0.949	0.001
Primate	0.83	1.26	0.1543	0.694	0.0007

Table 16. Chi square statistics comparing use versus availability of tiger prey in RNP.

Chital was the most utilized prey of tiger in RNP whereas Nilgai is marginally utilized. Primate and sambar were the least utilized prey of tiger in RNP respectively (Fig 10).

4.3.3 (c) Dietary overlap between Tiger and Leopard.

The dietary overlap between the tiger and leopard in the eastern sector of the park was very high with a mean of 0.91108 in Pianka's index as calculated by Ecosim 7 (Gotelli & Entsminger 2001). This shows that that they are more or less going for the same prey i.e. ungulates.

4.3.4 Spatial separation between Tiger and Leopard in Rajaji National Park

The two maps below (Fig. 16) and (Fig. 17) shows the generated density models for leopard and tiger and it could be clearly seen that the leopards are avoiding site where the intensity of space usage by tiger is high. The leopard space usage declines exponentially in the region where tiger movement is high.

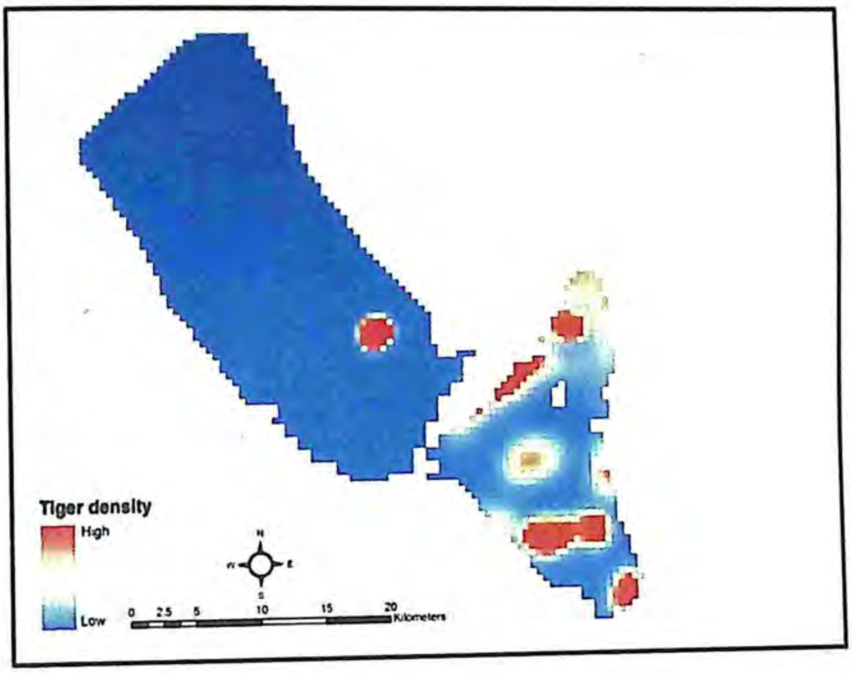


Fig 11: Activity centers of tigers in study area

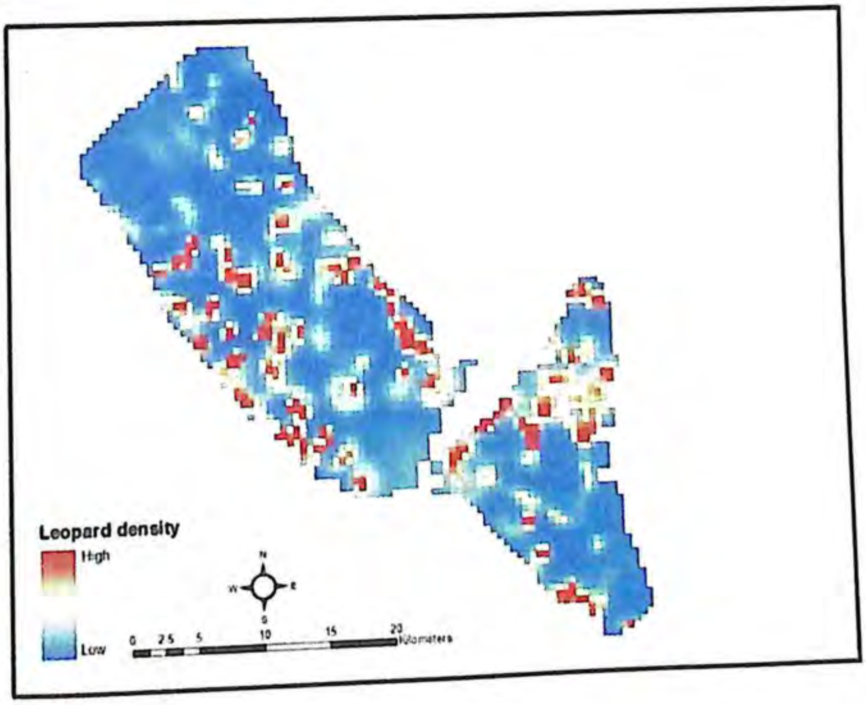


Fig 12: Activity centers of leopards in study area

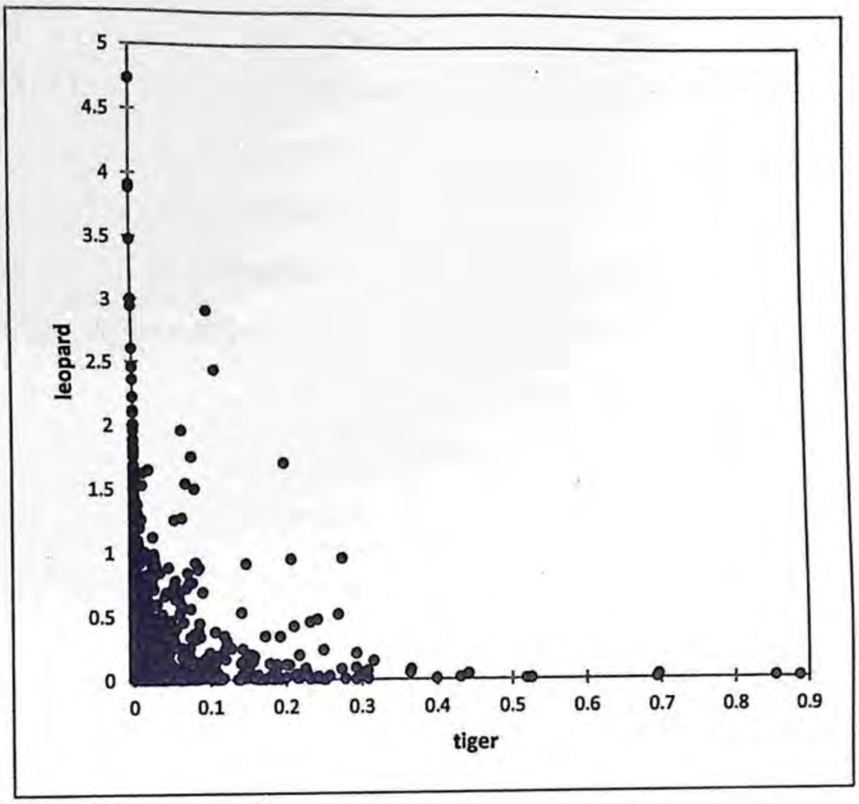


Fig 13. Scatter plot showing leopard vs. tiger density

After examining the scatter plot (Fig. 18) it is evident that high densities of leopard occurred at very low densities of tiger (exponential decay of leopard density toward high tiger density). Although there are some places where both leopard and tiger occurred at very low densities, which may be due to low prey availability, human disturbance and hostile terrain.

5. DISCUSSION

The tropical forests are known for their high prey densities (Karanth et al. 2004). My result corroborates this where both the sectors of RNP had high ungulate densities. The ungulate density is comparable and is not significantly different in either sector of the park. It reflects that both areas have a good potential to sustain reasonably high carnivore densities. This fact got further augmented by the large carnivore density estimates from my study. Leopard densities were very high with no significant difference in eastern and western sector (i.e. tiger occupied and non- tiger occupied areas). However, tiger density was moderate in eastern RNP but very low i.e. 0.28 ±0.23 /100 km^2 in western sector. This drastic difference in tiger density is due to the lack of functional connectivity between the two sectors of the park. Overall predator density is much higher in the eastern sector of the park. It seems that the tiger at a density of 3.03±0.95 /100 km^2 in the eastern sector are not enough to exert enough pressure on leopard which may reduce the absolute abundance of co-predator. The very small sigma value i.e. 0.73 km (an index of home range measures) for 85 % individuals indicate that leopards are moving in very small space to fulfill their basic resource needs like food, shelter and mate and thus the area is densely packed. Whereas, on the other hand the sigma value for tiger is 2.70 km i.e. almost four times of that leopard and it indicates that tiger are moving in much larger area to satisfy their needs for similar resources.

The major resource for large carnivores like tiger and leopard are food, cover, water, denning sites and mates. It is well known that the top-down effect increases with declining resources, which increases competition between sympatric species (Polis et al. 1989). For the above condition to meet the resource crunch should be for both the species and not just one of them. If this is the case then one of them will struggle to gain an excess to the resources while the other one will increase its abundance by exploiting the available resources. The intensity of this release depends upon the availability of resource (Elmhagen & Rushton 2007). In this very case of RNP the larger bodied tiger is exploring larger areas to meet it resource requirements but the leopard due to its behavioral plasticity, life history parameters and catholic diet seems to be exploiting the resource very well and thus co-existing with the tiger and becoming abundant (Hayward et al. 2006).

Apart from exploitative competition it is basically the encounter rate which leads to the competition in sympatric carnivore guild. These encounters may result in spatial and temporal segregation between the two species. High densities of the dominant predator may lead to higher encounter rates between them and the subordinate predators which may force the inferior one to avoid the sites (Ramesh et al. 2012). However, all the encounters between the two predators are not lethal but it is also a fact that the intensity of lethal encounters also increases with the increase in number of encounters. Since, the density of tiger (i.e. the dominant predator) is not high in RNP the frequency of interactions between the tiger and leopards are low and thus this led to increase in the abundance of leopard. The encounter rates and number of lethal encounters will increase when there is an increase in the density of apex-predator or the co-predator respectively. The difference in either situation is that when the density of the top-predator increases the number of lethal encounters increase thereby reducing co-predator density (Polis & Holt 1992; Laurenson 1995; Lindstro¨m et al. 1995). When the density of co-predator increases, the number of lethal encounters increases again but they might not be enough to bring a drastic change in the abundance of co-predator. Even if these interactions reduce the abundance of co-predator, it will lead to a decline in the encounter rates and the co-predator like leopard may flourish again due to its life history parameters. Along with this, the local ecological settings also play a key role in shaping up the predator community (Harihar et al. 2011).

Ecological impact of large carnivores is noticeable even at low densities (Wallach et al. 2010). The scale at which this will impact may change from place to place. Tiger with its larger body size dominates over leopard (Karanth & Sunquist 1995). Fatal interactions are infrequent in this community (Harihar et al. 2011) but the fear of being killed persuade the animal to avoid habitats where the larger predator is active (Lima & Dill 1990). In the case of my study in RNP it has been observed that although the tiger being the top carnivore in RNP is in moderate density in eastern sector and only two individuals in the western sector but they do have an influence on co-predator (i.e. leopard). The tigers even after being present in low density make the leopard to avoid its intensive use area at very fine scale. Leopard avoided the sites being used by tiger at very fine scale thereby again reducing the chances of lethal encounters between the two. This has helped leopard in successfully co-existing with tiger. Even the area used by the two tigress in western sector was less utilized by the leopard. This opens up a new window for the successful co-existence of leopard in presence of tigers. The interesting thing being that even low densities of top carnivore may alter the way of space use of sub-ordinate carnivore. This fine scale separation will again be a problem when the density of tiger increases in the area thereby increasing the encounter rates. Since the two are segregating in space then even their activity at same time won't be a problem for leopard.

The diet analysis done for the leopard in eastern and western sector of the park yielded different results. It shows that chital is the principal prey of leopard in the tiger occupied habitat (i.e. eastern sector) and sambar was the principal prey for leopard in the western sector (i.e. non- tiger occupied habitat). The result shows that leopard is going for larger bodied prey in absence of tigers. However, the reason behind higher sambar intake might be due to the habitat composition of northern slopes of western RNP. It is well known that habitat heterogeneity affects the intensity of prey predator interactions (Persson & Eklov 1995; Langellotto & Denno 2004). The reason for the higher sambar in the diet of leopard in western RNP may be due to the low interspersion of habitats and presence of homogeneous dense sal-dominated forest in a hilly terrain (i.e. non- chital habitat). Thus, chital is found in western sector but due to very low interspersion, their distribution is much more localized. The area is mostly hilly and is a typical sambar habitat. So, when a predator (i.e. leopard) moves in an area its encounters are more with sambar and not chital due to its localized distribution and movements. Therefore the presence of more sambar in diet of leopard might just be an artifact of habitat and not due to absence of larger predator (i.e. tiger). The principal prey of tiger was chital but sambar being almost equivalent to chital also formed major portion of tiger's diet. The reason for higher chital in diet is due to its higher abundance. The high proportion of sambar in diet of tiger might be due to larger gains provided by sambar for a large predator like tiger. Small prey formed very negligible portion of tiger's diet which still forms a significant proportion of leopard's diet. The high dietary overlap among leopard and tiger also indicate their dependency on similar food resources, but information from kills and direct observation is needed as they might be segregating at different age- structures of different prey species. The dietary overlap between the two was also very high. The study shows that although these two large carnivores have very high dietary overlap but they do segregate in space.

The study has created baseline data for predator and prey in RNP. There are plans of reintroducing tiger in the western sector of RNP. Our study clearly shows that tiger at co-exist with leopards in the eastern sector of the park. The abundance of principal prey of tiger is also high in western RNP. Thus, if the tiger is brought back in the western sector of the park, it would be of great ecological and conservational concern to see that how over time leopard and the prey are going to respond towards it.

LITERATURE CITED

Acharya BB. 2007. The ecology of the dhole or Asiatic wild dog (*Cuon alpinus*) in Pench Tiger Reserve, Madhya Pradesh (Doctoral dissertation, Wildlife Institute of India).

Ackerman BB, Lindzey FG & Hemker TP. 1984. Cougar food habits in southern Utah. The Journal of Wildlife Management, 48, 147–155.

Andersen DC, Wilson KR, Miller MS, Falck M. 2000. Movement patterns of riparian small mammals during predictable floodplain inundation. J. Mammalogy., 81: 1087-1099.

Andheria AP, Karanth KU, & Kumar NS. 2007. Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. Journal of Zoology, 273(2), 169-175.

Bagchi S, Goyal SP & Sankar K. 2003. Prey abundance and prey selection by tigers (Panthera tigris) in a semi-arid, dry deciduous forest in western India. Journal of Zoology, 260(03), 285-290.

Bailey TN. 1993. The African leopard: ecology and behavior of a solitary felid. New York: Columbia University

Balme GA, Hunter LTB, Slotow R. Evaluating methods for counting cryptic carnivores. J Wildl Manage. 2009. 73: 433–441.

Bertram BCB. 1999. Leopard. In The encyclopedia of mammals: 44–48. Macdonald, D.W. (Ed.). Oxford: Andromeda Oxford Limited.

Beschta RL. & Ripple WJ. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation,142(11), 2401-2414.

Biswas S & Sankar K. 2002. Prey abundance and food habit of tigers (Panthera tigris tigris) in Pench National Park, Madhya Pradesh, India. Journal of Zoology, 256(03), 411-420.

Borchers DL & Efford MG. 2008. Spatially explicit maximum likelihood methods for capture–recapture studies. Biometrics, 64(2), 377-385.

Breitenmoser U. 1998. Large predators in the Alps: the fall and rise of man's competitors. Biological Conservation, 83(3), 279-289.

Brown WL & Wilson EO. 1956. Character displacement. Syst. Zool., 5, 49–64.

Bruno JF & Cardinale BJ. 2008. Cascading effects of predator richness. Frontiers in Ecology and the Environment, 6(10), 539-546.

Buckland ST, Anderson DR., Burnham, KP, Laake JL, Borchers DL & Thomas L. 2001. Introduction to distance sampling: estimating abundance of wildlife populations. Introduction to distance sampling: estimating abundance of wildlife populations.

Burnham KP, Anderson DR and Laake JL. 1980. Estimation of density from line transect sampling of biological populations. Wildlife Monographs. 72:1-202.

Burnham KP & Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.

Carbone C, Mace GM, Roberts SC & Macdonald DW. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature, 402(6759), 286-288.

Carbone C & Gittleman JL. 2002. A common rule for the scaling of carnivore density. Science 295, 2273–2276.carnivores. Biological Conservation 110:67-75.

Cardilla M, Purvis A, Sechrest W, Gittleman JL, Bielby J & Mace GM. 2004. Human population density and extinction risk in the world's carnivores. PLoS biology, 2(7), e197.

Cardilla M, Mace GM, Jones KE, Bielby J, Bininda-Emonds OR, Sechrest W & Purvis A. 2005. Multiple causes of high extinction risk in large mammal species. Science, 309(5738), 1239-1241.

Caro TM & Stoner CJ. 2003. The potential for interspecific competition among African carnivores. Biological Conservation, 110(1), 67-75.

Ceballos G, Erlich PR, Soberon J, Salazar I & Fay JP. 2005. Global mammal conservation: What must we manage? Science, 309, 603–607.

Chakrabarti S, Jhala YV, Qureshi Q .2013. Computing biomass consumption from prey occurrences in scats of tropical felids. (Masters Dissertation, Wildlife Institute of India).

Champion HG, Seth SK .1968. The forest types of India. Nasik, India: Manager, Government of India press. 404 p.

Chesson J. 1978. Measuring preference in selective predation. Ecology, 211-215.

Chesson PL. 1986. Environmental variation and the coexistence of species. Community Ecology (eds J. Diamond & T.J. Case), pp. 240 –256. Harper and Row, New York, USA.

Crall, JP, Stewart CV, Berger-Wolf TY, Rubenstein DI & Sundaresan SR. .2013, January. HotSpotter—Patterned species instance recognition. In Applications of Computer Vision (WACV), 2013 IEEE Workshop on (pp. 230-237). IEEE.

Creel S. 2001. Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. Conservation Biology 15:271–274.

Creel S, Christianson D, Liley S & Winnie JA. 2007. Predation risk affects reproductive physiology and demography of elk. Science, 315(5814), 960-960.

Creel S, Spong G. & Creel NM. 2001. Interspecific competition and the population biology of extinction-prone carnivores. Carnivore Conservation (eds J.L. Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), pp. 35–60. University of Cambridge, Cambridge.

Crooks KR and Soule′ ME. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Dalerum F, Somers MJ, Kunkel K & Cameron EZ. 2008. The potential for large carnivores to act as biodiversity surrogates in southern Africa.Biodivers.Conserv. 17:2939–2949.

Dayan T & Simberloff D. 2005. Ecological and community-wide character displacement: the next generation. Ecology Letters, 8(8), 875-894.

Dayan T, Simberloff D, Tchernov E & Yom-Tov Y. 1990. Feline canines: community-wide character displacement in the small cats of Israel. Am. Nat., 136, 39–60.

Di Bitetti MS, De Angelo CD, Di Blanco YE & Paviolo A. 2010. Niche partitioning and species coexistence in a Neotropical felid assemblage. Acta. Oecol. 36, 403–412.

Dillon A, Kelly MJ. Ocelot Leopardus pardalis in Belize: the impact of trap spacing and distance moved on density estimates. Oryx. 2007. 41: 469–477.

Dillon A, Kelly MJ. Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. J Zool. 2008. 275: 391–398.

Dinerstein E. 1997. A framework for identifying high priority areas and actions for the conservation of tigers in the wild. World Wildlife Fund-US.

Durant SM. 1998. Competition refuge and coexistence: an example from Serengeti carnivores. Journal of Animal Ecology 67:370 386.

Eaton RL. 1979. Interference competition among carnivores: a model for the evolution of social behavior. Carnivore, 2(9-16), 82-90.

Edgaonkar A. 2008. Ecology of the leopard (Panthera pardus) in Bori wildlife sanctuary and Satpura national park, India (Doctoral dissertation, University of Florida).

Efford M. 2004. Density estimation in live-trapping studies. Oikos, 106(3), 598-610.

Efford MG, Borchers DL, Byrom AE .2009. Density estimation by spatially explicit capture–recapture: likelihood-based methods. In: DL ThomsonEG CoochMJ Conroy. Modelling demographic processes in marked populations. New York: Springer. pp. 255–269. 43.

Efford MG, Dawson DK, Borchers DL .2009. Population density estimated from locations of individuals on a passive detector array. Ecology 90: 2676-2682. doi:10.1890/08-1735.1. PubMed: 19886477.

Efford .MG. 2011. Estimation of population density by spatially explicit capture-recapture analysis of data from area searches. Ecology, 92(12), 2202-2207.

Elmhagen B, Rushton SP. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecol. Lett. 10, 197–206.

Emmons LH. 1989. Jaguar Predation on Chelonians. Journal of Herpetology 23: 311-314

Emmons LH. 1987. Co mparative feeding ecology of felids in a neotropical rainforest. Beh avioral Ecology and Sociobology 20: 271-283

Estes JA Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ & Wardle DA. 2011. Trophic downgrading of planet Earth. science, 333(6040), 301-306.

Finke DL & Denno RF. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. Ecol. Lett.8: 1299–1306.

Finke DL & Denno RF. 2006. Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. Oecologia, 149(2), 265-275.

Finlayson GR, Vieira EM, Priddel D, Wheeler R, Bentley JM & Dickman CR. 2008. Multi-scale patterns of habitat use by reintroduced mammals: a case study using mediumsized marsupials. Biol. Conserv. 141: 320–331.

Floyd TJ, Mech LD, & Jordan PA. 1978. Relating wolf scat content to prey consumed. The Journal of Wildlife Management, 528-532.

Foster RJ, Harmsen BJ, Doncaster CP. 2010. Habitat use by sympatric jaguars and pumas across a gradient of human disturbance. Biotropica 42: 724-731

Gause GF. 1934. "'The Struggle for Existence.'" Baltimore: Williams and Wilkins.

Gittleman JL. 1989. Carnivore group living: comparative trends. In Carnivore behavior, ecology, and evolution (pp. 183-207). Springer US.

Gittleman JL. 1985. Carnivore body size – ecological and taxonomic correlates. Oecologia, 67, 540–554.

Gittleman JL. 1989. Carnivore group living: comparative trends. In Carnivore behavior, ecology, and evolution (pp. 183-207). Springer US.

Gopalaswamy AM, Royle JA, Hines JE, Pallavi S, Jathanna D et al. 2011. SPACECAP: A Program to Estimate Animal Abundance and Density using Bayesian Spatially-Explicit Capture-Recapture Models. Wildlife Conservation Society - India Program, Centre for Wildlife Studies, Bengaluru, India. (Version 1.0.6)

Gotelli NJ. and Entsminger GL. 2001. EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. http://homepages.together.net/~gentsmin/ecosim.htm

Grant PR. 1972. Convergent and divergent character displacement. Biol. J. Linn. Soc., 4, 39–68.

Haemig PD. 2012 Sympatric Tiger, Leopard and Dhole. ECOLOGY.INFO 22

Harihar A, Pandav B, Goyal SP. 2009a. Responses of tiger (Panthera tigris) and their prey to removal of anthropogenic influences in Rajaji National Park. Indian Eur. J. Wildlife Res. 55, 97–105.

Harihar A, Prasad DL, Ri C, Pandav B & Goyal SP. 2009b. Losing ground: tigers *Panthera tigris* in the north-western Shivalik landscape of India. Oryx, 43(01), 35-43.

Harihar A, Pandav B, Goyal, SP. 2011. Responses of leopard Panthera pardus to the recovery of a tiger Panthera tigris population. J. Appl. Ecol. 48, 806–814.

Harihar A & Pandav B. 2012. Influence of connectivity, wild prey and disturbance on occupancy of tigers in the human-dominated western Terai Arc Landscape. PloS one, 7(7), e40105.

Harmsen BJ, Foster RJ, Silver SC, Ostro LET, Doncaster CP. 2009. Spatial and temporal interactions of sympatric jaguars (Panthera onca) and Pumas (*Puma concolor*) in a Neotropical forest. Journal of Mammalogy 90: 612-620

Harrington LA, Harrington AL, Yamaguchi N, Thom MD, Ferreras P, Windham TR, and Macdonald. DW. 2009. The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression? Ecology 90:1207–1216.

Harvey CT & Eubanks MD. 2005. Intraguild predation of parasitoids by *Solenopsis invicta*: a non-disruptive interaction. Entomologia experimentalis et applicata, 114(2), 127-135.

Hayward MW and Slotow R. 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. South African Journal of Wildlife Research 39:109–125.

Hayward MW, Adendorff J, O'brien J, Sholto-Douglas A, Bissett C, Moolman LC, Bean P, Fogarty A,

Howarth D, Slater R & Kerley GIH. 2007a. The reintroduction of large carnivores to the Eastern Cape Province, South Africa: an assessment. Oryx 41: 205–214.

Hayward MW & Kerley GI. 2008. Prey preferences and dietary overlap amongst Africa's large predators. South African Journal of Wildlife Research, 38(2), 93-108.

Hayward MW, Henschel P, O'brien J, Hofmeyr M, Balme G & Kerley GI. H. 2006. Prey preferences of the leopard (Panthera pardus). Journal of Zoology, 270(2), 298-313.

Hayward MW, Jędrzejewski W & Jedrzejewska B. 2012. Prey preferences of the tiger Panthera tigris. Journal of Zoology, 286(3), 221-231.

Hayward MW & Hayward GJ. 2007. Activity patterns of reintroduced lion Panthera leo and spotted hyaena Crocuta crocuta in Addo Elephant NationalPark, South Africa.Afr.J.Ecol. 45:135–141.

Heilbrun RD, Silvy NJ, Peterson MJ, Tewes ME. Estimating bobcat abundance using automatically triggered cameras. Wildl Soc Bull. 2006; 34: 69–73.

Heithaus MR. 2001. Habitat selection by predators and prey in communities with asymmetrical intraguild predation. Oikos 92, 542–554.

Hunter LT. 1998. The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, KwaZulu-Natal, South Africa (Doctoral dissertation, University of Pretoria).

Holt RD, Polis, GA. 1997. A theoretical framework for intraguild predation. Am. Nat. 149, 745–764.

Hutchinson GE. 1959. Homage to Santa Rosalia or why are there so many kinds of animals?. American naturalist, 145-159.

IUCN 2010. The IUCN Red List of Threatened Species. <http://www.iucnredlistorg>. Janssen A., Sabelis, M.W., Magalhaes, S., Montserrat, M., Van der Hammen, T., 2007. Habitat structure affects intraguild predation. Ecology 88, 2713–2719.

Ivlev VS. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven.

Jackson RM, Roe JD, Wangchuk R, Hunter DO. Estimating snow leopard population abundance using photography and capture-recapture techniques. Wildl Soc Bull. 2006; 34: 772–781.

Jethva BD & Jhala YV. 2004. Computing biomass consumption from prey occurrences in Indian wolf scats. Zoo Biology, 23(6), 513-520.

Johnsingh AJT, 1983. Large mammalian prey-predators in Bandipur. Journal of the Bombay Natural History Society, 80: 1-57.

Johnsingh AJT & Negi AS. 2003. Status of tiger and leopard in Rajaji–Corbett Conservation Unit, northern India. Biological Conservation, 111(3), 385-393.

Johnsingh AJT, Ramesh K, Qureshi Q, David A, Goyal SP, Rawat GS & Prasad, S. 2004. Conservation status of tiger and associated species in the Terai Arc Landscape, India (pp. viii+-110). Dehradun: Wildlife Institute of India.

Johnsingh AJT. 1992. Prey selection in three sympatric carnivores in Bandipur. Mammalia 56, 517–526.

Johnson WE & Franklin WL. 1994. Spatial resource partitioning by sympatric grey fox (Dusicyon griseus) and culpeo fox (Dusicyon culpaeus) in southern Chile. Canadian Journal of Zoology, 72(10), 1788-1793.

Karanth KU & Chellam R.2009. Carnivore conservation at the crossroads. Oryx, 43(1), 1-2.

Karanth KU & Sunquist ME. 1995. Prey selection by tiger, leopard and dhole in tropical forests. Journal of Animal Ecology, 439-450.

Karanth KU, Nichols JD. 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862

Karanth KU & Sunquist ME. 1992. Population structure, density and biomass of large herbivores in the tropical forests of Nagarahole, India. Journal of Tropical Ecology, 8(01), 21-35.

Karanth KU & Sunquist ME. 2000. Behavioural correlates of predation by tiger (Panthera tigris), leopard (Panthera pardus) and dhole (Cuon alpinus) in Nagarahole, India. Journal of Zoology, 250(02), 255-265.

Karanth KU, Chundawat RS, Nichols JD & Kumar N. 2004. Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture–recapture sampling. Animal Conservation, 7(3), 285-290.

Karanth KU, Nichols JD, Kumar NS, Hines JE .2006. Assessing tiger population dynamics using photographic capture–recapture sampling. Ecology 87: 2925–2937. Available online at: doi: 10.1890/0012-9658(2006)87[2925:ATPDUP]2.0.CO;2. PubMed: 17168036

Kruuk H. (1972). Surplus killing by carnivores. Journal of Zoology, 166(2), 233-244.

Langellotto GA & Denno RF. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia, 139(1), 1-10.

Lamprecht J. 1981. The function of social hunting in larger terrestrial carnivores. Mammal Review, 11(4), 169-179.

Laurenson MK. 1995. Implications of high offspring mortality for cheetah population dynamics. Pages 385–399 in A. R. E. Sinclair and P. Arcese, eds. Serengeti II: dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68, 619–640.

Lindstro¨m, ER, Brainerd SM, Helldin JO and. Overskaug K. 1995. Pine marten–red fox interactions: a case of intraguild predation? Annales Zoologici Fennici 32:123–130.

Linnell J and Strand O. 2000. Interference interactions, coexistence and conservation of mammalian carnivores. Diversity and Distribution 6:169–176.

Linnell JD, Swenson JE & Anderson R. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Animal Conservation, 4(4), 345-349.

Macdonald DW. 1983. The ecology of carnivore social behaviour. Nature, 301(5899), 379-384.

MacNally RC. 1983. On assessing the significance of interspecific competition to guild structure. Ecology, 64: 1646-1652.

Majumder A, Sankar K, Qureshi Q & Basu S. 2013. Predation ecology of large sympatric carnivores as influenced by available wild ungulate prey in a tropical deciduous forest of Central India. Journal of Tropical Ecology, 29(05), 417-426.

Mills MGL & Harvey M. 2001. African predators. Cape Town: Struik.

Mills MGL, Mills MEJ. 1982. Factors affecting the movement patterns of brown hyaenas, Hyaena brunnea, in the southern Kalahari. South African Journal of Natural Research 12, 111–117.

Mondal K, Gupta S, Bhattacharjee S, Qureshi Q & Sankar K. 2012. Response of leopards to re-introduced tigers in Sariska Tiger Reserve, Western India. Int J Biodivers Conserv, 4(5), 228-236.

Morin P. 1999. Community Ecology. Blackwell Science, Oxford.

Morrison JC, Sechrest W, Dinerstein E, Wilcove DS & Lamoreux JF. 2007. Persistence of large mammal faunas as indicators of global human impacts. Journal of Mammalogy, 88(6), 1363-1380.

Mukherjee S, Goyal SP & Chellam R. 1994a. Standardisation of scat analysis techniques for leopard (Panthera pardus) in Gir National Park, Western India.Mammalia, 58, 139–144.

Mukherjee S, Goyal SP & Chellam R. 1994b. Refined techniques for the analysis of Asiatic lion Panthera leo persica scats. Acta Theriologica, 39, 425430 .

Nowell K. & Jackson P. 1996. Wild cats: status, survey and conservation action plan. Gland, Switzerland: IUCN/ Species Survival Commission Cat Specialist Group.

Otis DL, Burnham KP, White GC & Anderson DR. 1978 Statistical inference from capture data on closed animal populations. Wildlife Monographs, 62, 1–135.

Owen-Smith N & Mills MGL. 2008. Predator–prey size relationships in an African large-mammal food web. J. Anim. Ecol. 77: 173–183.

Palomares F, Gaona P, Ferreras P & Delibes M. (1995). Positive effects on game species of top predators by controlling smaller predator populations: an example with lynx, mongooses, and rabbits. Conservation Biology, 9(2), 295-305.

Palomares F, Ferreras P, Fedriani JM & Delibes M. 1996. Spatial relationships between Iberian lynx and other carnivores in an area of south-western Spain. Journal of Applied Ecology, 5-13.

Palomares F and Caro TM. 1999. Interspecific killing among mammalian carnivores. American Naturalist 153:492–508.

Pandey S, Joshua J, Rai ND, Mohan D, Rawat GS, Sankar K, Katti MV, Khati DVS, Johnsingh AJT. 2004. Birds of Rajaji National Park, India. Forktail. 10 (5): 105-113.

Petren K, Case TJ. 1998. Habitat structure determines competition intensity and invasion success in gecko lizards. PNAS, 95: 11739- 11744.

Pianka ER. 1973.The structure of lizard communities. Annual Review of Ecology and Systematics, 4, 53–74.

Pianka ER. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences USA 71:2141–2145.

Polis GA, Myers CA, Holt RD, 1989. The ecology and evolution of intraguild predation. Annu. Rev. Ecol. Syst. 20, 297–330.

Polis GA & Holt RD. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology & Evolution, 7(5), 151-154.

Preisser EL, Bolnick DI & Benard MF. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology, 86(2), 501-509.

Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS & Brashares JS. 2009. The rise of the mesopredator. Bioscience, 59(9), 779-791.

Purvis AJL, Gittleman G, Cowlishaw and Mace GM. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society B 1456:1947–1952.

Ralls K & Harvey PH. 1985. Geographic variation in size and sexual dimorphism of North American weasels. Biol. J. Linn. Soc., 25, 119–167.

Ramakrishnan U, Coss RG & Pelkey NW. 1999. Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. Biological Conservation, 89(2), 113-120.

Ramesh T, Kalle R, Sankar K & Qureshi Q. 2012. Spatio-temporal partitioning among large carnivores in relation to major prey species in Western Ghats. Journal of Zoology, 287(4), 269-275.

Ramesh T, Snehalatha V, Sankar K & Qureshi Q. 2009. Food habits and prey selection of tiger and leopard in Mudumalai Tiger Reserve, Tamil Nadu, India. Journal of Scientific Transactions in Environment and Technovation, 2, 170-181.

Ramesh T. 2010. Prey selection and food habits of large carnivores (tiger, leopard and dhole) in Mudumalai Tiger Reserve, Western Ghats, India.PhD thesis, Saurastra University, Rajkot, India. 178 pp.

Reynolds JC & Aebisher NJ. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox Vulpes vulpes. Mammal Review, 21(3), 97-122.

Ripple WJ & Beschta RL. 2006. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. Biol. Conserv. 133: 397–408.

Ripple WJ & Beschta RL. 2007. Restoring Yellowstone's aspen with wolves. Biol. Conserv. 138: 514–519.

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M & Wirsing AJ. 2014. Status and ecological effects of the world's largest carnivores. Science, 343(6167), 1241484.

Ritchie EG & Johnson CN. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology letters, 12(9), 982-998.

Ritchie EG, Elmhagen B, Glen AS, Letnic M, Ludwig G & McDonald RA. 2012. Ecosystem restoration with teeth: what role for predators?. Trends in Ecology & Evolution, 27(5), 265-271.

Rosenzweig ML. 1991. Habitat selection and population interactions: the search for mechanism. The American Naturalist, 137, S5–S28.

Royle JA, Karanth KU, Gopalaswamy AM & Kumar NS. 2009. Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. Ecology, 90(11), 3233-3244.

Royle JA, Young KV .2008. A hierarchical model for spatial capturerecapture data. Ecology 89: 2281–2289. doi:10.1890/07-0601.1. PubMed: 18724738.

Sankar K, Qureshi Q, Nigam P, Malik PK, Sinha PR, Mehrotra RN, Gopal R, Bhattacharjee S, Mondal K, Gupta S. 2010. Monitoring of reintroduced tigers in Sariska Tiger Reserve, 32 Western India: Preliminary findings on home range, prey selection and food habits. J. Trop. Conserv. Sci., 3(3): 301-318

Sankar K & Johnsingh AJT. 2002. Food habits of tiger (Panthera tigris) and leopard (Panthera pardus) in Sariska Tiger Reserve, Rajasthan, India, as shown by scat analysis. Mammalia, 66(2), 285-289.

Sankar K. 1994. The ecology of three large sympatric herbivores (chital, sambar, nilgai) with special reference for reserve management in Sariska Tiger Reserve, Rajasthan. Ph. D. Thesis, University of Rajasthan, Jaipur.

Hines JE. 2002. SCATMAN. Version 2.0 USGS-PWRC.

Schaller GB. 1967. The deer and the tiger: A study of wildlife in India. University Chicago Press, Chicago. 370 pp.

Schipper J, Chanson JS, Chiozza F, Cox NA, Hoffman M, Katariya V. et al. 2008. The status of the world's land and marine mammals: diversity, threat and knowledge. Science, 322, 225–230

Schoener TW. 1974a. Resource partitioning in ecological communities. Science 185, 27–39.

Scognamillo DG, Maxit IE, Sunquist M, Polisar J. 2003. Coexistence of Jaguar (Panthera onca) and Puma (Puma concolor) in a mosaic landscape in the Venezuelan llanos. Journal of the Zoological Society of London 259: 269-279

Seidensticker J. 1976. On the ecological separation between tigers and leopards. Biotropica, 225-234.

Selvan KM, Veeraswami GG, Lyngdoh S, Habib B & Hussain SA. 2013. Prey selection and food habits of three sympatric large carnivores in a tropical lowland forest of the Eastern Himalayan Biodiversity Hotspot. Mammalian Biology-Zeitschrift für Säugetierkunde, 78(4), 296-303.

Simberloff D, Dayan T, Jones C & Ogura G. 2000. Rapid character displacement and release in the small Indian mongoose, Herpestes javanicus. Ecology, 81, 2086–2099.

Slotow R & Hunter LTB. 2009. Reintroduction decisions taken at the incorrect social scale devalue their conservation contribution: African lion in South Africa. In: M.W. Hayward & M.J. Somers (Eds), The reintroduction of top-order predators (pp. 43–71). Wiley-Blackwell Publishing, Oxford.

Soisalo MK, Cavalcanti S. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. Biol Conserv. 2006. 129: 487–496.

Southwell C & Weaver K. (1993). Evaluation of analystical procedures for density estimation from line-transect data: data grouping, data truncation and the unit of analysis. Wildlife Research, 20(4), 433-443.

Steinmetz R, Seuaturien N & Chutipong W. 2013. Tigers, leopards, and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. Biological Conservation, 163, 68-78.

Sunquist ME. 1981. The social organization of tigers (Panthera tigris) in Royal Chitawan National Park, Nepal (p. 107). Washington, DC, USA:: Smithsonian Institution Press.

Sunquist ME, Karanth KU & Sunquist F. 1999. Ecology, behaviour and resilience of the tiger and its conservation needs. In Riding the tiger: tiger conservation in human dominated landscapes: 5–18. Seidensticker, J., Christie, S. & Jackson, P. (Eds). Cambridge: Cambridge University Press.

Sunquist F, Sunquist M. 2002. Tiger moon: tracking the great cats of Nepal. University of Chicago Press, USA.

Swenson JE, Sandegren F & SO-Derberg A. 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. Journal of Animal Ecology, 67(5), 819-826.

Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL & Burnham, KP. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology, 47(1), 5-14.

Uniyal S, Agrawal S, Rana MS, Verma YS. 2006. Bibliography on Rajaji National Park, Envis Bulletin : Wildlife and Protected Areas, Vol 9.

Vanak AT, Fortin D, Thaker M, Ogden M, Owen C, Greatwood S & Slotow R. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. Ecology, 94(11), 2619-2631.

VanValkenburgh B & Wayne RK. 1994. Shape divergence associated with size convergence in sympatric East-African jackals. Ecology, 75, 1567–1581.

Venkataraman AB. 1995. Do dholes (*Cuon alpinus*) live in packs in response to competition with or predation by large cats?. Current science, 69(11), 934-936.

Vucetich JA and Creel S. 1999. Ecological interactions, social organization, and extinction risk in African wild dogs. Conservation Biology 13:1172–1182.

Wallach AD, Johnson CN, Ritchie EG & O'Neill AJ. 2010. Predator control promotes invasive dominated ecological states. Ecology letters, 13(8), 1008-1018.

Walters C.1986. Adaptive management of renewable resources. Macmillan, New York.

Wang SW, Macdonald DW. 2009. Feeding habits and niche partitioning in a predator guild composed of tigers, leopards and dholes in a temperate ecosystem in central Bhutan. Journal of Zoology 277: 275-283

White PJ & Garrott RA. 1997. Factors regulating kit fox populations. Canadian Journal of Zoology, 75(12), 1982-1988.

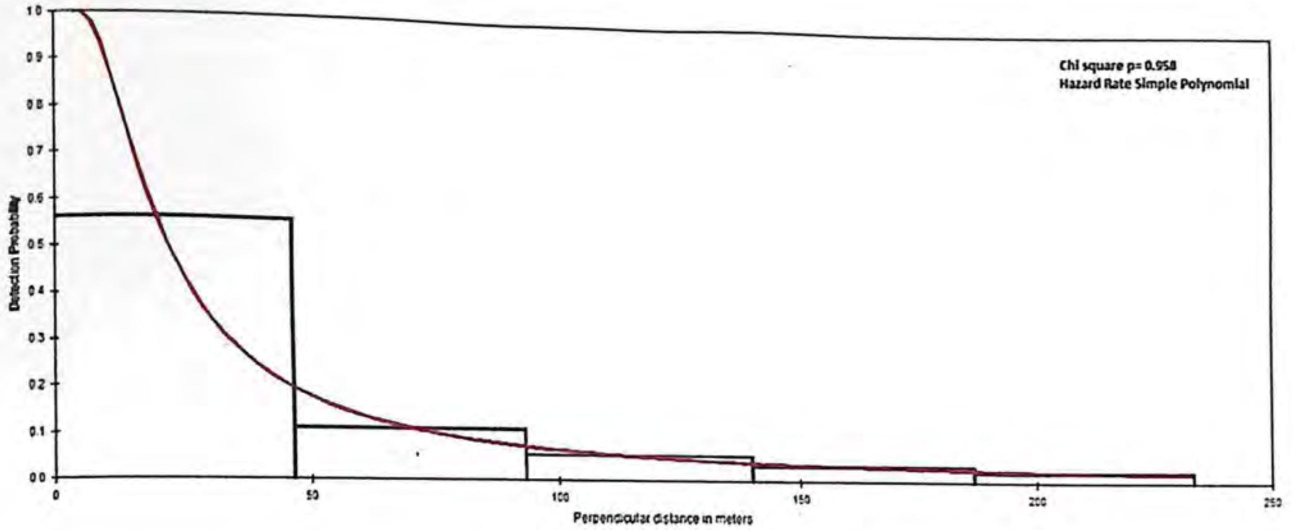
Woodroffe R & Ginsberg JR. 1998. Edge effects and the extinction of populations inside protected areas. Science, 280(5372), 2126-2128.

Warfe DM & Barmuta LA. 2004. Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia, 141(1), 171-178.

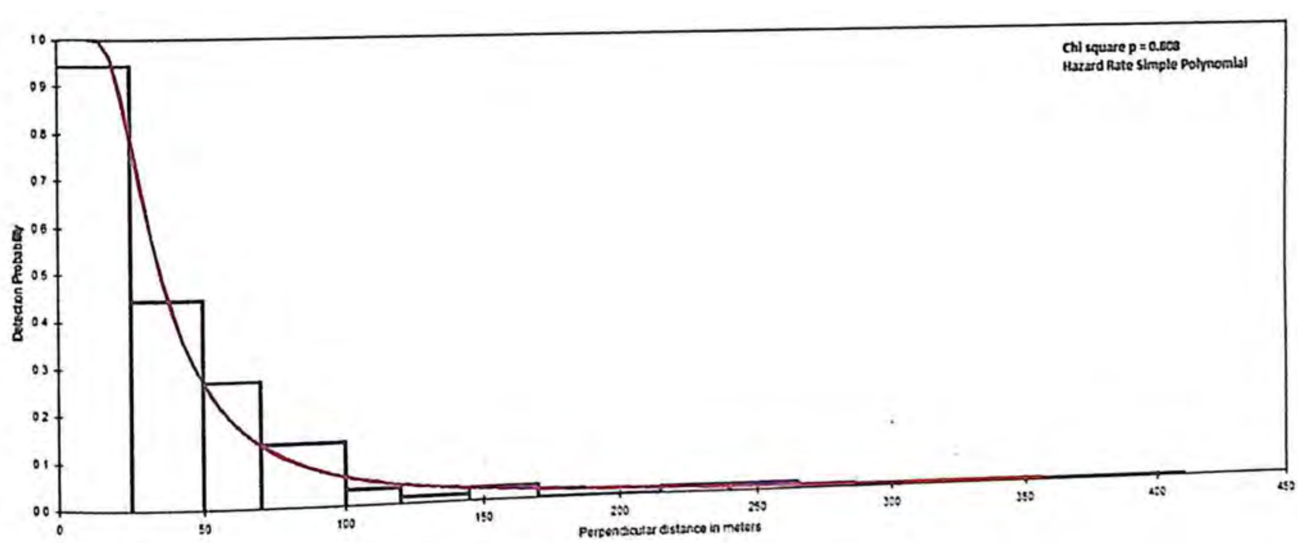
Xiaoming W, Tedford RH, Van Valkenburgh B & Wayne RK. 2004. Phylogeny, classification, and evolutionary ecology of the Canidae. In:C. Sillero-Zubiri, M. Hoffman & D.W. Macdonald (eds), Canids:

foxes, wolves, jackals and dogs. Status survey and conservation action plan (pp. 8–20). IUCN/SSC Canid Specialist Group, Gland, Switzerland and Cambridge, U.K.

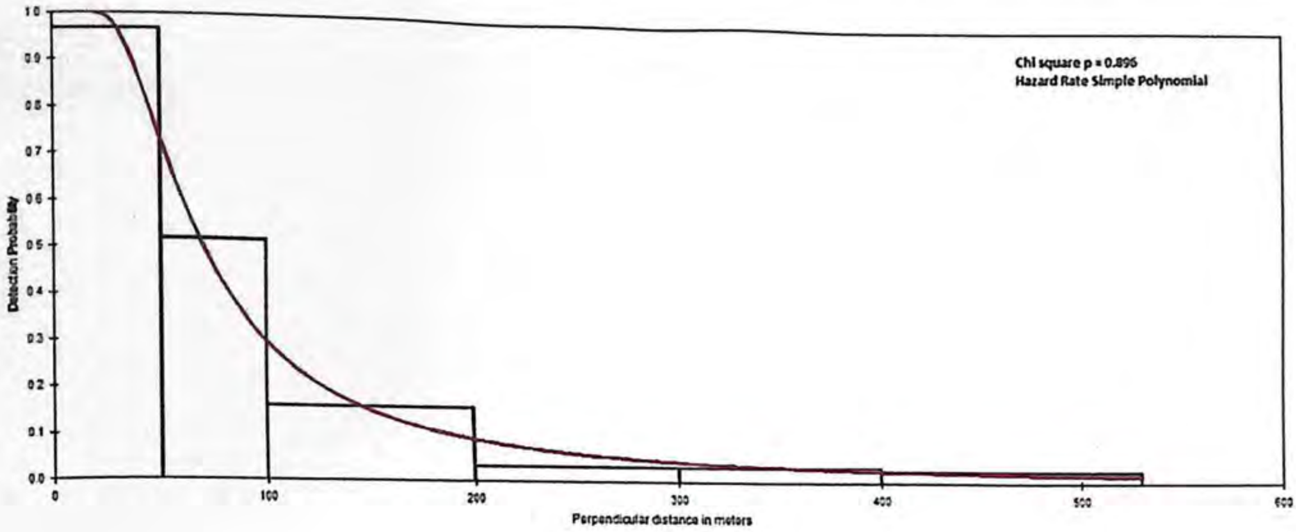
Appendix



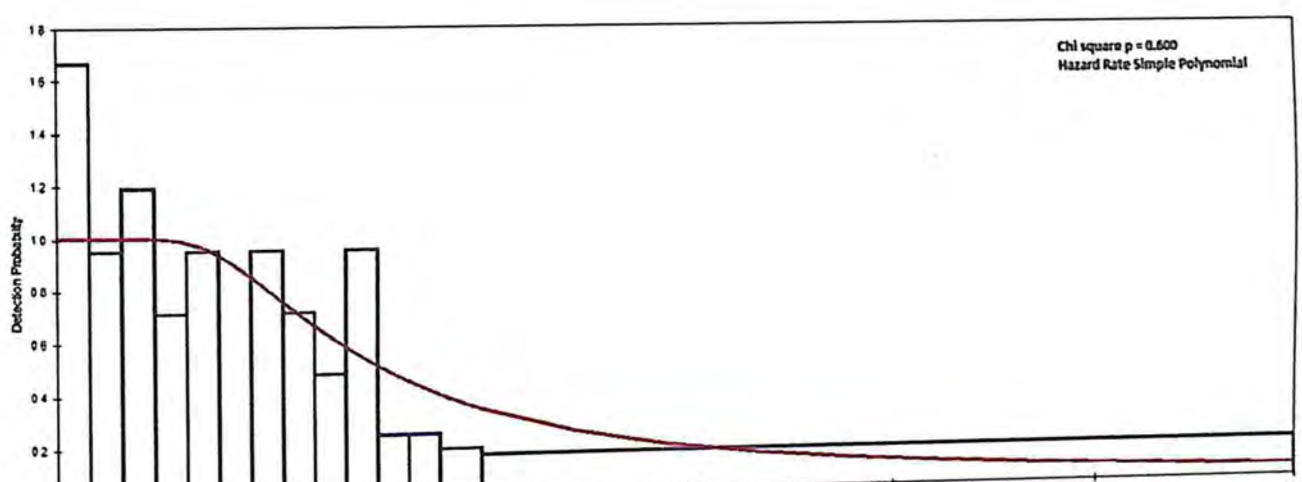
Detection function curve of Chital in Eastern RNP



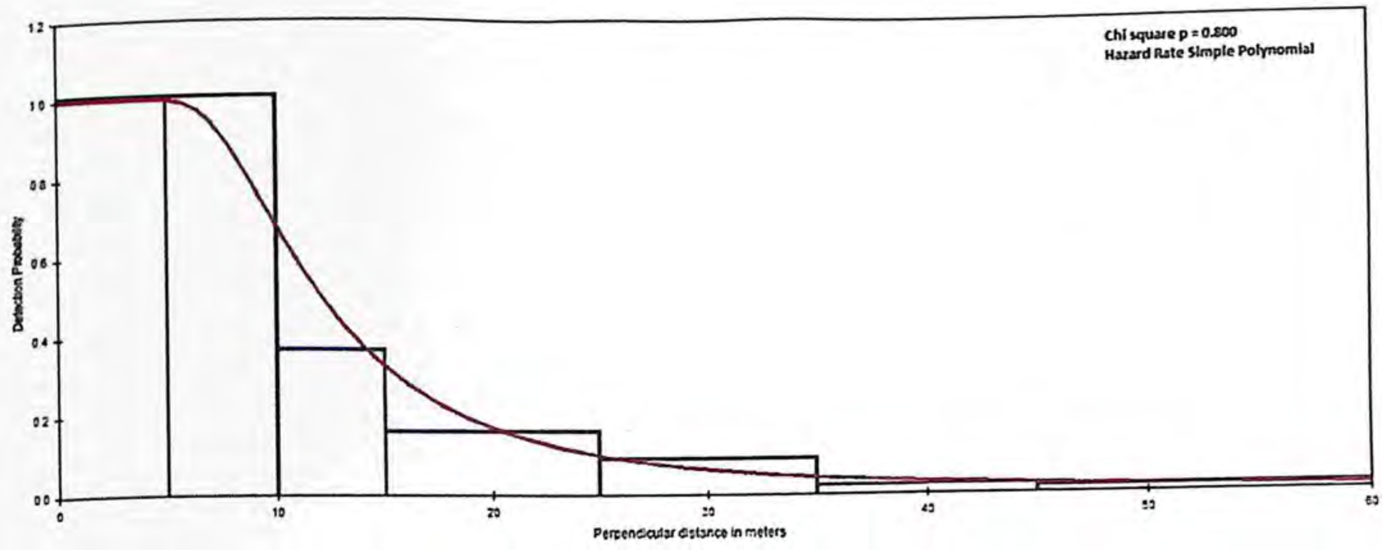
Detection function curve of Chital in Western RNP



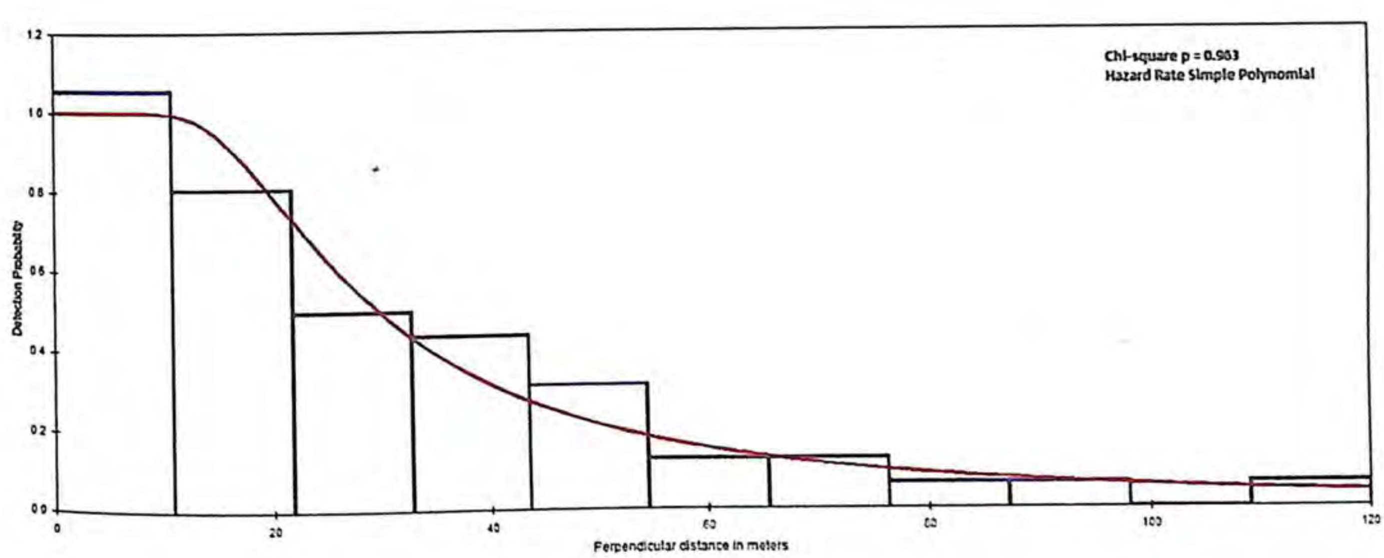
Detection function curve of Nilgai in Eastern and Western RNP



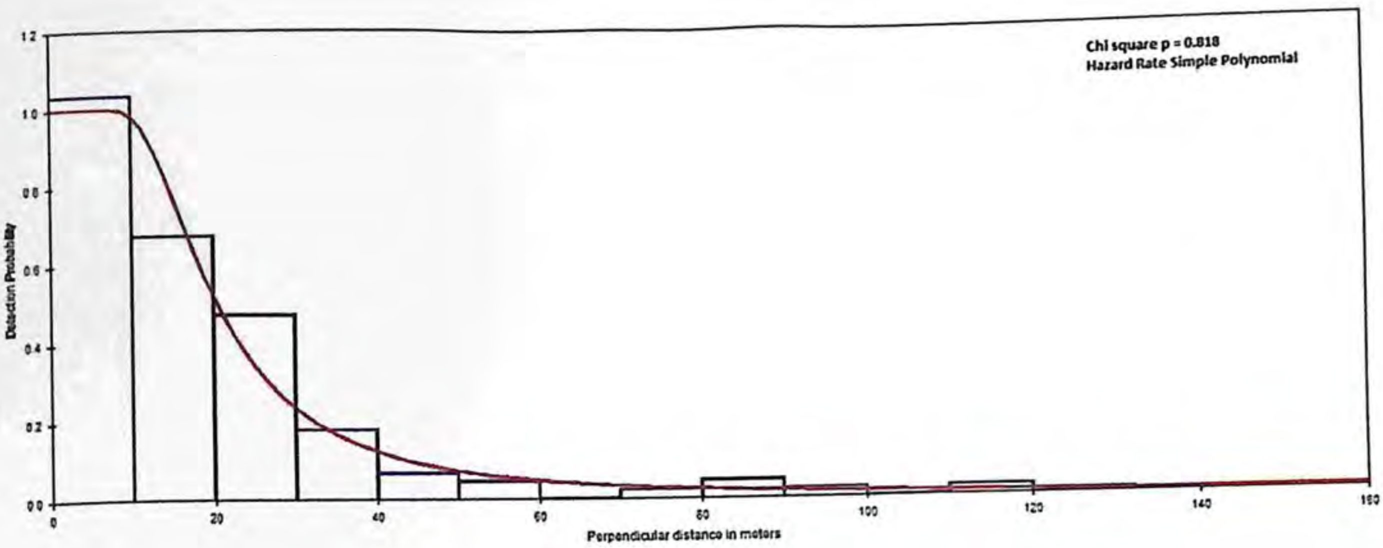
Detection function curve of Primate in Eastern and Western RNP



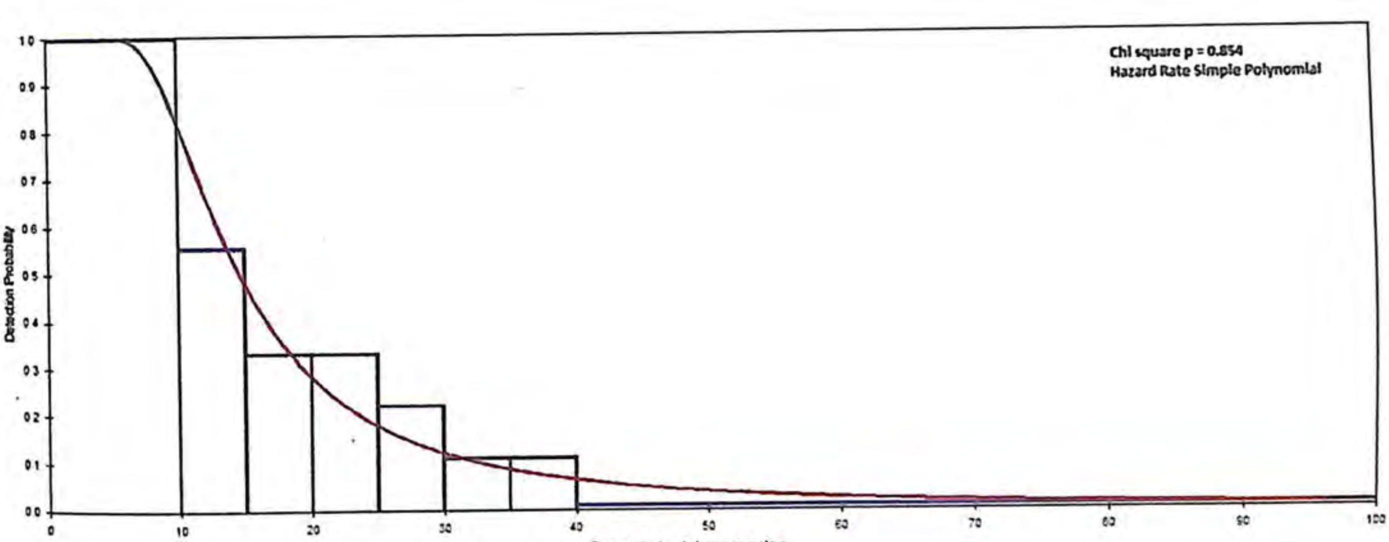
Detection function curve of Primate in Eastern and Western RNP



Detection function curve of Sambar in Eastern RNP



Detection function curve of Primates in Eastern and Western RNP



Detection function curve of Wild Pig in Eastern and Western RNP