Tiger and Leopard: Population ecology and resource partitioning of sympatric carnivores in Kanha Tiger Reserve M.P.

A THESIS
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Under the guidance of

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Declaration by the Candidate

I declare that the thesis entitled ***Tiger and Leopard: Population ecology and resource partitioning of sympatric carnivores in Kanha Tiger Reserve M.P.*** submitted by me for the degree of Doctor of Philosophy is the record of research work carried out by me during the period from **2012 to 2019** Under the guidance of **Y.V. Jhala** and **Q. Qureshi** and has not formed the basis for the award of any degree, diploma, associate ship, fellowship, titles in this or any other University or other institution of higher learning. I further declare that the material obtained from other sources has been duly acknowledged in the thesis. I shall be solely responsible for any plagiarism or other irregularities, if noticed in the thesis.

Signature of the Candidate:

Place: Dehradun Date : 23rd July 2019

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SUMMARY

1. Large investment in the form of protected areas, human resettlement, law enforcement-patrols and habitat management are made to conserve tigers and reap their benevolent umbrella role to secure India’s biodiversity. Tigers and leopards share their entire range except in mangrove forest of Sundarbans in India. Their populations are under severe threat across the entire range, primarily because of poaching and habitat fragmentation. Both carnivores shape the ecosystem function by virtue of their top position in the food chain. In spite of their ecological importance, there are limited studies on their long-term population ecology and co-existence. To best plan conservation strategies at the landscape level, it is crucial to understand the population dynamics of tiger and leopard. Hence, I attempted to study (i) the trend of tiger and leopard population (ii) demography of tigers and leopards and mechanism of their co-existence.
2. My study area was Kanha tiger reserve (area 2074 km^2), a major stronghold for both species in central Indian landscape. The tiger reserve has two-management units core zone (917 km^2) devoid of human settlements and a multiple use buffer zone (1165 km^2) comprised by revenue and protected forests and agriculture fields. The core zone, which is also called as Kanha National Park, is part of two river catchments Banjar and Halon. Camera trap based mark-recapture framework were used to estimate population dynamics

(densities, population trend survival and recruitment) of tigers and leopards. Camera traps were placed in the dirt road, animal trails and riverbeds to maximize the capture of tiger and leopards. Initial two years (2011-2012) the sampling area were small as 280 km^2 in Banjar catchment and 180 km^2 in Halon catchment (with one camera station in 4-5 km^2) but later from 2013 to 2017 with extra resources I was able to sample entire core zone (917 km^2) with high camera trap densities (with one camera station in 1-2 km^2).

3. Population trends of the threatened species are required for evaluating the success of management actions and prioritizing conservation investments. Densities of tigers and leopards, their sex ratios and population trend over six years were estimated through multisession maximum likelihood based spatially explicit capture recapture models (secr). SECR has two basic parameters i) g_0 the detection at activity centre and ii) σ the spatial scale of detection e.g. movement parameter. I accounted for major potential sources of variability in the data by modelling g_0 and σ as a function of gender and sampling year (as density was likely to change between years and potentially alter σ). Tiger density of Kanha PA (at 100 km^{-2}) ranged from 4.82 ± 0.33 to 5.21 ± 0.55 and the leopard densities (at 100 km^{-2}) varied between 6.63 ± 0.71 to 8.64 ± 0.75. Overall sex ratio in Kanha National Park (M:F) was biased towards females for both tigers (0.66 ± 0.03) and leopards (0.50 ± 0.02). The density for both tigers and leopards in Banjar catchment showed growth with a $\lambda = 1.10$ ($CI_{95\%}$ 1.02-1.18) for tigers and $\lambda = 1.15$, ($CI_{95\%}$ 1.05-1.27) for

leopards. While for the Halon catchment tiger and leopard density remained stable at $\lambda = 0.98$ ($CI_{95\%}$ 0.86-1.14) and $\lambda = 1.09$ ($CI_{95\%}$ 0.98-1.22). Tiger and leopard densities were stable at the PA scale but I found at the local scale Banjar catchment that had had higher prey density and high conservation investments, recorded significant growth for both carnivores. While Halon catchment that had low prey and lower investments, tiger and leopard populations were stable.

4. Key vital rates such as reproductive parameters and survival rates are important to device recovery strategies for endangered carnivores. I estimated vital parameters of tiger demography through robust design based classical open population models in which population was open to demographic process (recruitment, deaths, immigration and emigration) during the period of 7 years (2011-2017) from 147 adult tigers (>1 year) and by collating information on survival and reproductive parameters by regular monitoring of 127 known tigers from all age groups. I estimated mean litter size (n=31) to be 3.24 (± 0.63), inter birth interval (n=29) to be 22 ± 2.7 months, age of first reproduction (n=11) to be 3.30 ± 0.13 years. Age specific survival estimates was the lowest for cubs (0.59 ±0.06), and highest for adult stage (3-10 years) e.g. for males (0.87 range 0.69 -0.95) and females (0.92 range 0.80-0.97). Female showed higher survival throughout their adult stages. Male tigers exhibited a typical Type II survivorship curve while survivorship of tigresses was a curve between Type I & II. The apparent survival from robust design

camera trap based open population model was also female-biased (0.84 ±0.03) compared to male (0.78 ± 0.05). Since I had estimates of actual adult gender specific survival from the same population contemporaneously from known fate models along with apparent survival obtained by camera trap based robust design, I could estimate emigration (dispersal) for each gender in adult tigers. I estimated that about 9% of males and 8% of females annually dispersed outside to the study area and repopulate the nearby tiger landscape. Results of this study concede the importance of wildlife corridors between protected areas for long-term survival. Kanha is the largest source population in central India and well connected to the Pench, Achannakmar, Navegaon Nagzira tiger reserves.

5. Leopard is one of the most widespread carnivores but information on population dynamics such as survival and reproductive parameters are remarkable scares. Demographic parameters for leopards through camera trap based studies was challenging since they have low detection rate in camera traps resulting zero inflated capture-recaptures, especially in the areas where they share their resources to congeneric large carnivores. The density and other population parameters estimate based on low detection rate are imprecise and of limited value. By experience gained in initial three years, I increased camera densities to better optimize for leopard detections. The classical open population Non-spatial models are sensitive to zero-inflated capture-recaptures resulting parameters un-identifiability and imprecise estimates.

Non-spatial models cannot differentiate between mortality and emigration, but the Bayesian spatial open population models allow to model the movement and separate emigration from mortality, they provide more realistic estimates of demographic parameters with fewer restrictive assumptions. In this study, I used Bayesian open population spatial capture recapture models to estimate demographic parameters such as sex specific survival, recruitment and population growth rate for the leopard. Contrary to expectation, the survival estimates were low for females (0.69 range 0.61 – 0.75) compared to males (0.83 range 0.76 – 0.91) in leopards. The sex ratio was overall female biased throughout the sampling years. Average recruitment rate in the population was high for female (0.29 range 0.22 – 0.35) and low for male (0.07 range 0.04 – 0.10); this likely suggests a scenario where low survival but higher proportion in the population and high recruitment is possible when sex ratio at birth is skewed towards females. The high mortality of female was compensated by higher recruitment rate to give female-biased sex ratios. This could be likely a function of high tiger density in the PA, and female leopards are more vulnerable to intraspecific predation by tiger due to their small size, small home range and higher spatial philopatry.

6. Sympatric species of similar guilds can potentially compete for resources such as food and space. Tigers co-occur with the leopards in their entire range except in mangrove forest of Sundarbans in India. Both top predators have similar diets. Tiger and leopard co-exist together by resource partitioning on

the scale of space, time and diet. In this study, I investigated the mechanism of co-existence of both predators. For spatial partitioning spatial densities were estimated through secr model for of both the species. To understand how leopard population responds to tiger densities and growth at the scale home range size of breeding tigress (10 km^2), growth rate were estimated for both the carnivores by regressing ln(density) against year. Contour plots for leopard growth rates against tiger density and against tiger growth rates were drawn in NCSS to evaluate the demographic response of leopards to tiger demography. I found that at tiger home range scale (10 km^2 grids), leopards achieved high density in areas with medium or declining tiger density. Leopard populations showed growth in areas with low to medium-stable tiger density or declining tiger density. I also evaluated the response of predator densities with increasing distance from PA boundary. Tiger densities steeply declined with the increasing distance from protected area, leopards, known to be better adapted to survive near humans use buffer zone without exhibiting multi-modal density declines as seen in tigers.

7. To assess the temporal activity pattern of tiger and leopards in Kanha tiger reserve, I used time of photo-capture obtained from the camera trap pictures. I found tigers and leopards were primarily nocturnal with high overlap in activity (86% range 83 -89). I collected scats of both the predator to assess the diet and I found high overlap in diet composition. The mechanism of diet overlap and coexistence is related to high and diverse prey availability in

Kanha tiger reserve, which is likely to be associated with habitat heterogeneity. The heterogeneous habitat with ample prey facilitates coexistence between these two carnivores

8. This was the first study which used both camera trap based mark-recapture and continuous monitoring known fate information to estimate reproductive parameters along with age specific survival and dispersal probability of tigers. First study on leopards for estimating sex-specific actual survival and recruitment rate using novel non-invasive open population spatial capture recapture models. Such information is crucial to develop conservation strategies for these threatened carnivores.

CHAPTER 1 : INTRODUCTION & STUDY AREA

1.1 Tiger and Leopard: Current status and distribution:

Tiger *Panthera tigris* and leopard *Panthera pardus* have iconic status due to their apex predator position in the food chain, serve as umbrella species for biodiversity conservation at landscapes scales (Albert, Luque, & Courchamp, 2018). Tigers were historically distributed from the Caucasus Sea to Caspian Sea, Siberia, Bali- Indonesia, the Philippines, Borneo and Palawan (Tilson & Seal, 1988). Currently, distribution of tiger has reduced to include only India, Southeast Asia, Western China and some eastern Russian regions. However, tigers have lost 93% of their former range which spread across 13 countries (Sanderson et. al. 2006). The Bengal tiger (*Panthera tigris. tigris*) inhabits parts of India, Bangladesh, Nepal and Bhutan. India is home to world's 75% of the wild tigers despite having a growing human population over a billion. Currently tiger occurs largely in the forest areas of 19 states in India. While, leopard is the more common and has an extensive spread across Africa, and Asia from the Middle East till Pacific Ocean (Hunter & Barrett, 2014.; Nowell & Jackson, 1996; Sunquist & Sunquist, 2002). Leopard can persist in areas due to behavioral plasticity while other large carnivores (tigers and lions) from these areas are eliminated (Athreya et al., 2014). However, despite its adaptability, leopards are declining across their range (Athreya et al., 2014). However, despite its adaptability, leopards are declining across their range (Ripple et al., 2014).).

Information on range-wide population estimate of leopards is lacking due to limited field data on distribution status and population size (Jacobson et al., 2016).

The World conservation union (IUCN) classifies the Indian leopard as near threatened and Tiger as endangered in India (Goodrich et al., 2015; Stein et al., 2016). Major threat to both tiger and leopard includes habitat loss and fragmentation, prey depletion, conflict with people, unsustainable trophy hunting, poaching for body parts, and indiscriminate killing (Raza et al., 2012; Swanepoel et al., 2015). It is therefore important to have a regular update on the status of the tigers, leopards, and their prey in their natural habitats. These estimates guide the needs for immediate protection, management and development of predators' habitat with an aim to reduce trade, and prevention of human–wildlife conflicts.

1.2 Tiger and Leopard: Population ecology

Prey density is an important determinant of carnivore density which influences carnivore's territory size in terms of optimal expenditure of energy, density of breeding females, number of transients, reproduction and survival of cubs and juveniles(Carbone, Teacher, & Rowcliffe, 2007). Prey size adds further dimensions in explaining the structure of predators, considering the optimal foraging theory in terms of size and number of a particular prey individuals (Nyhus & Tilson, 2004). Studies have shown strong positive relationships between abundance of large ungulates and tiger densities (Karanth et al., 2004). However, by virtue of being the apex predator density of tigers even in high prey biomass areas are low(Karanth & Sunquist, 2000). Tiger and Leopard range nocturnally and widely, making observations difficult in the wild. In the past few years, the population analysis methods have progressed significantly, this has permitted researchers to deal with both statistical and biological complications of sampling endangered and elusive species (Thompson, 2004). Since tiger and leopard, can both be uniquely identified through their natural pelage pattern, hence camera trap based mark-recapture framework can be used to estimate the abundance of these carnivores. Karanth, (1995) first used this method to estimate the tiger population under closed mark-recapture framework (Otis et al., 1978). Later, this sampling method was effectively used to estimate carnivore abundance across the world (Karanth & Nichols, 1998; Azlan & Sharma, 2003; O'Brien, Kinnaird, & Wibisono, 2003; Soisalo & Cavalcanti, 2006). However, these closed population studies are limited to snapshot population estimation. Information on population parameters such as survival, recruitment and dispersal are not available from this approach and are therefore sparce. Long-term camera trap based studies can provide better insight on tiger and leopard demography. So far very few studies using camera traps have been done for the long-term but see (Karanth, et al., 2006; Duangchantrasiri et al., 2016; Bisht et al., 2019). However, Camera Trap based demographic parameters cannot distinguish between dispersal and mortality and lump these as apparent survival (Schaub & Royle, 2013).While continuous monitoring of individually known animals through radio-telemetry and/or by other means which permits the researcher to determine the fate of the animal, provides a correct estimate of survival by differentiating between mortality and dispersal (Smith & McDougal, 1991; Kerley et al., 2003; Sadhu et al., 2017). However, till date there has been no study of a carnivore population where demographic information is simultaneously obtained with both approaches i.e. camera trapping and individual known animal monitoring. Though, several studies provide information on tiger demography using camera traps (Karanth et al., 2006; Duangchantrasiri et al., 2016; Bisht et al., 2019)and known fate(Smith & McDougal, 1991; Goodrich et al., 2008; Sadhu et al., 2017), information on leopard demography is completely lacking.

1.3 Tiger and Leopard: Resource partitioning between sympatric carnivores

Tigers and leopards are top carnivores, which are often sympatric in the forested landscapes of India. The coexistence of similar trophic sympatric species is facilitated by ecological separation along minor differences in the trophic niche, and spatial and temporal dimensions of their environment (Pianka, 1973; Melero, Palazon, & Gosalbez, 2008), and differential habitat use (Thomas W Schoener, 1971).

Competitive interactions can be an important factor in shaping species abundance. Ecologically dominant carnivores influence recruitment and the population dynamics of subordinate species through both direct predation and competition for shared resources (Laurenson, 1995; S Creel, 2001; Switalski, 2003). When top carnivore populations are reduced either through natural population fluctuations or human exploitation, other sympatric carnivore can become functionally released from competition which can have ramifications for lower trophic levels(Rogers & Caro, 1998; Crooks & Soulé, 1999; Berger, Swenson, & Persson, 2001) These relationships broadly termed intraguild competition, can take the form of exploitative competition or interference competition. In exploitative competition animals compete indirectly for a finite resource - a food item consumed by one individual cannot be consumed by another and a den site that can only be occupied by one animal at a time(Jaeger, 1974). In contrast, interference competition takes place when two animals compete directly for a resource, especially food, and can result in the death of one of the competitors (Linnell, Strand, & Landa, 1999). There have been several attempts to use theoretical models to illustrate the interspecific relationships that are most likely to facilitate species coexistence (e.g. Polis et al. 1989, Holt and Polis 1997, Křivan 2000, Revilla 2002, Roth et al. 2008). There are many studies which indicate that leopards avoid tigers as inference made by Karanth & Sunquist, (2000) from their studies in Nagarhole National Park, India, but concurs with observations in Chitwan National Park, Nepal (Seidensticker, 1976; McDougal, 1988). The differing results imply that the behaviour of the two species differs according to the ecological settings of the study area, and that there is no single ‘‘key to co-existence’’ between tigers and leopards. Aspects like habitat preferences and selection (Donnelly & Marzluff, 2004; Gray, Anderson, & Benecha, 2007) are of great significance in species survival, since such information offers opportunity for informed decisions pertaining to the conservation and management of the habitats preferred by species. Study by Harihar, Pandav, & Goyal, (2011) in Rajaji National Park indicates that indirect mechanisms such as restricted habitat use and avoidance by leopards to tigers could be important in controlling the distribution and abundance of leopards. Differences among sympatric species with respect to use of trophic niche, temporal, and spatial aspects of their environments have frequently been used to clarify how the component species coexist (Navarro et al., 2013). Segregation along one or more of these niche dimensions facilitates partitioning of resources and thereby the ecological separation of species (Karanth and Sunquist 2000). Niche is defined herein as an n-dimensional hypervolume, in which each dimension represents a resource or condition of importance for the species, and habitat is defined as a set of physical variables (i.e. vegetation, elevation, prey etc.) within the niche's hypervolume (Begon, Townsend, & Harper, 2006.). The competitive exclusion principle defines that two ecologically similar species cannot coexist (Hardin, 1960). Thus, some degree of partitioning has to occur in species realized niche, which can occur at the trophic level. Studies in niche separation between competing species have hitherto dealt with trophic niche overlap or differential habitat use, for instance with use vs. availability designs (Serafini & Lovari, 1993; Lanszki et al., 1999; Baghli & Verhagen, 2004).

Among mammalian carnivore interspecific competition and abundance (Scott Creel, 2001; Palomares & Caro, 1999) was found to be an important ecological factor in shaping species composition and whether the separation is causally related to competitive interactions, due to stochastic effects, or to other structuring factors has, however, been the subject of some debate (Wiens, 1977; Schoener, 1983) Habitat loss combined with decreasing prey numbers can intensify sympatric competition for food and space in predator guilds(Wiens, 1993). Under these circumstances, knowledge of intraguild competition, prey selection and niche partitioning will be useful for guiding management of these sympatric carnivores in landscapes.

1.3 Questions and Objectives:

The majority of information on tiger demographic parameters are available in parts, from different studies like apparent survival and recruitment from Karanth, et al. (2006), now Duangchantrasiri, et al (2017) and Bisht, et al (2019) and reproductive parameters and age specific true survivals from comes from Smith and McDougal (1998) and Sadhu, et al (2017). Since tigers are widely distributed in the forested landscape of India, demographic parameters may vary between the different climates, habitats, prey densities, and other environmental parameters. Information on leopard demography is completely absent. Since Kanha tiger reserve is the major strong hold both the carnivores. Therefore, I studied population dynamics & resource partitioning of these co-predators in Kanha Tiger Reserve. Based on this background, I have attempted to answer following questions:

1. What is the trend in the population of tigers and leopards in a) Kanha tiger reserve and b) Different parts of the reserve, which differ in prey abundance and conservation investments?
2. How do tigers and leopards partition space and time and select prey?
3. What are the demographic parameters such as density, sex ratio, proportion of breeding females, survival, recruitment, and dispersal of tigers and leopards in Kanha tiger reserve?

To answer above questions, my study objectives were as follows:

1. To estimate the demographic parameter of tiger and leopard in Kanha Tiger Reserve,

    a) Annual abundance i.e. population size and density and b) Survivorship

2. To estimate the resource utilization and resource partitioning of Tiger and Leopard in Kanha tiger reserve for understanding the mechanism permitting co-existence between them.

1.4 Study Area:

Kanha Tiger Reserve nestled on the northern slopes of the Maikal hills of the Satpuras in Deccan plateau of Central Indian highlands, and within Mandla and Balaghat districts of Madhya Pradesh, India between 22^{o} 02’ 52.6” and 22^{o} 25’ 48.8” latitude and 80^{o} 30’ 09.3” an 81^{o} 02’ 48.4” longitude (Figure 1.1).

Kanha Tiger Reserve covers an area of 2074 sq. km. of which 940 sq. km. comprises of National Park and 1134.31 km^2 is the buffer zone. Within the National Park, 917.43 km^2 of area has been notified as the core zone or Critical Tiger Habitat. The core area of the tiger reserve covers the catchments of two rivers Banjar and Halon. A narrow ridge of Bhaisanghat separates these two catchments. Banjar and Halon valleys, named after the respective rivers, and forming the western and eastern part of the tiger reserve. These two catchments were acclaimed countrywide as excellent *shikar* blocks in the 1930s, parts of these valleys later moved up in conservation status and became wildlife sanctuaries and later jointly formed the present National Park.

Since its inception as a national park in 1955, the Banjar catchment gained considerable conservation investment in terms of village relocation and habitat management compared to Halon catchment, which was added to the National Park in 1976. The potential of tiger conservation was so great that the National Park was also among the first nine to be included in the ambitious Project Tiger scheme in 1973. The Banjar catchment has high prey densities, less anthropogenic pressure due to absence of villages inside and more flat terrain compared to Halon catchment (Negi & Shukla, 2011). By 2016, most of the villages from Halon catchment were also relocated and conservationists are hopeful for prey recovery. The overall ungulates prey density of Kanha National Park is 50±4.6/km^2, one of the highest prey densities in Asia with an average biomass (in kg) of 26,806, ± 2573/ km^2 (Awasthi et al., 2016). The entire National Park is a Reserved Forest with three sub-divisions and six forest ranges while buffer zone consists of forest land, revenue land and private holdings. Except for some of the eastern part, the buffer zone almost completely surrounds the National Park. Administratively, there are two sub-divisions and five forest ranges in buffer zone. There are three distinct seasons in Kanha Tiger Reserve viz. Summer, March to mid-June (the hottest period extends from late April to the first week of June). Monsoon, Mid-June to late September (July and August are the wettest months, and the average annual rainfall is around 1200 mm) and winter, November to February (with night temperature dropping to -20C at times during December and January).

The vegetation of Kanha Tiger Reserve falls under two types (Champion & Seth, 1968): Moist Sal Forests (3C/C2), with subgroups High level Sal (3C/C2 ci) and Low level Sal (3C/C2 cii); and Miscellaneous Forests (3A/C2), with subgroups Southern tropical Moist Deciduous Forest, Southern tropical Dry Mixed Deciduous Forest and Grassland The Major tree species are Sal (*Shorea robusta*), Saja (*Terminalia alata*), Lendia (*Lagerstroemia parviflora*), Dhawa (*Anogeissus latifolia*), Tendu (*Diospyros melanoxylon*), Palash (*Butea monosperma*), Bija (*Pterocarpus marsupium*), Mahua (*Madhuca indca*), Aonla (*Phyllanthus emblica*), and Bamboo (*Dandrcalamus strictus*) etc. Besides there are many species of climbers, forbs and grasses. Among the carnivoes Tiger (*Panthera tigris*), Leopard (*Panthera pardus*), Sloth bear (*Melursus ursinus*), Wild dog (*Cuon alpinus*), Jackal (*Canis aureus*), Fox (*Vuples bengalensis*) and small Indian Civet (*Viverricula indica*). Among the ungulates, Chital (*Axis axis*), Sambar (*Rusa unicolor*), Barasingha (*Rucervus duvaucelli branderi*), Barking deer (*Muntiacus vaginalis*), Chousingha (*Tetracerus quadricorni*s), Gaur (*Bos gaurus*) and wild pig (*Sus scrofa*) are commonly found. Other mammals include Langur (*Semnopithecus enetellus*) and ruddy mongoose (*Herpestes* spp.) Kanha Tiger Reserve is inhabited by traditional tribal community such as Gonds and Baigas since historic times.

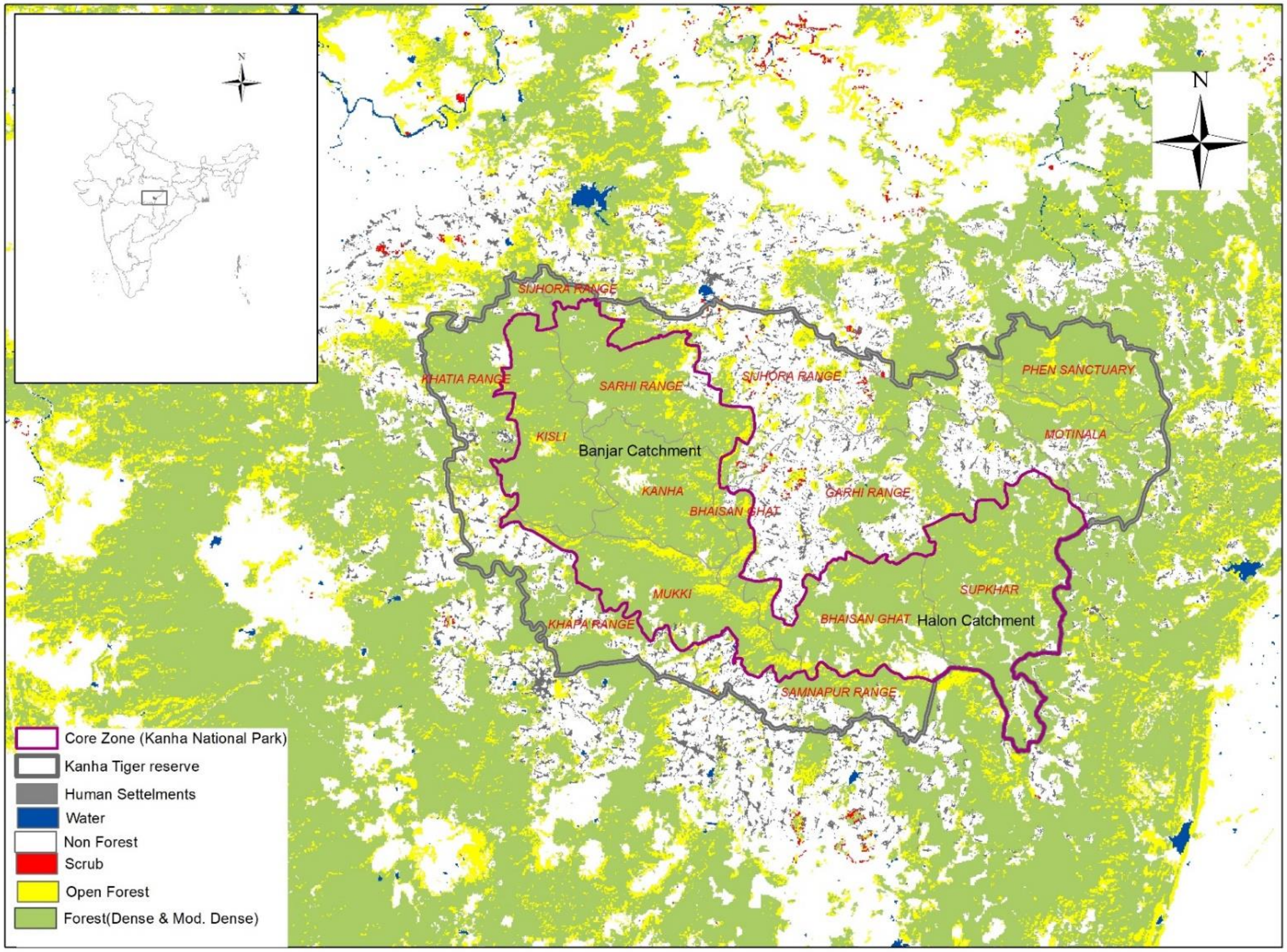

Figure 1. 1 Area (Kanha Tiiger Reserve)

CHAPTER 2. POPULATION TREND OF TIGERS AND LEOPARDS

2.1 Introduction:

The endangered tiger, once widely distributed in Asia has now lost 93% of its former range, currently occurring in 10 countries (Verheij, Foley, & Engel, 2010) India holds the most abundant wild tiger population estimated at about 70% of the global population (Jhala, Qureshi, & Gopal, 2015). Tiger serves as an umbrella and charismatic species for the conservation of tropical forest in Asia and prefers undisturbed habitats with large prey(Karanth & Sunquist, 1995). The leopard is most widely distributed across much of Africa and forested landscape of Asia. It's status less precarious compared to tiger, which shared its range in Asia. Despite leopard has wider distribution and being a habitat and prey generalist but even population is declining due to poaching and habitat loss (Bailey, 2005). These two carnivores coexist together in much of the forested landscape of Asia (Johnsingh & Negi, 2003; Stein et al., 2016). Abundance estimates and population trend of the threatened species are required for evaluating the success of management actions and prioritizing conservation measures (Krebs, 2001). In spite of their ecological importance, there are limited studies on their long-term population trends (Durant et al., 2011). Development of camera trapped based mark-recapture alias classical non-spatial closed capture method was the primary choice for estimating abundance of uniquely identified species (Otis et al., 1978; Karanth & Nichols, 1998). These species were uniquely identified through their pelage patterns such as tiger (Karanth & Nichols, 1998), Jaguar (Silveira et al., 2010), Leopard (Harihar, Pandav, & Goyal, 2011), and Ocelots (Trolle & Kery, 2003).

Albeit tiger is extensively studied in terms of population and status, (Karanth & Nichols, 1998; Jhala, Qureshi, & Gopal, 2015; Kawanishi & Sunquist, 2004; Aziz et al., 2017), studies on leopard abundance and distribution are relatively scarce (but see- Harihar, Pandav, & Goyal, 2011; Kalle et al., 2011). Information on demographic parameters also lacks since most studies are limited to snapshot population estimation. Most population trend studies on tigers used either classical non-spatial closed capture-recapture models (Karanth & Nichols, 1998; Harihar, Pandav, & Goyal, 2011) or statistically less rigorous track counts (Miquelle et al., 2015) to estimate the population trends. Classical capture mark recapture uses an ad-hoc buffer to estimate effective sampling area; hence, density estimates can be biased (Soisalo & Cavalcanti, 2006). While spatially explicit capture-recapture (SECR) especially accounts for space through a spatial point process, thereby modelling density directly from spatial capture locations (Borchers & Efford, 2008; Royle et al., 2009). With the development of SECR models in the last decade, the monitoring of big carnivores using SECR models has gained considerable impetus. Later SECR models were refined by incorporating sex-specific heterogeneity in detection functions (Sollmann et al., 2011).

In this study, the tiger and leopard densities, sex ratios and their trend over six years were estimated in Kanha National Park Madhya Pradesh India a major stronghold for both species in Central India**.**

2.2 Methodology:

Camera trap based mark-recapture framework (Karanth, 1995) was used to estimate spatially explicit densities of tiger and leopard (Borchers & Efford, 2008). The sampling area was divided into two regions the Banjar and Halon catchments due to logistic constraint, the difference in prey densities and conservation investments. In the initial two years 2011 to 2012 sampling areas was smaller, an area of 280 km^2 in Banjar valley and 180 km^2 in Halon Valley with average trap spacing of 1.8 km. Later from 2013 to 2016 with extra resources, I was able to sample the entire core area of 916 km^2 (Figure 2.1). From experience, it was learnt that leopards did not get sufficient capture recaptures for precise abundance estimation when camera traps were optimized for tiger. This was because leopards likely had smaller home ranges and were more “trap shy”. Hence, camera densities were increased by reducing inter trap distance (Table 2.1). Extensive sign surveys were conducted to select the best possible location of camera traps. Camera traps were placed on the forest roads, animal trails and dry streams that were intensively used by tigers and leopards to maximize the detections (Karanth and Nichols, 1998). Individual tigers and leopards were identified through their pelage pattern with the assistance of Program Extract Compare (Hiby et al., 2009)and Hotspotter respectively(Crall, J. et al., 2013).

Maximum likelihood-based spatially explicit capture-recapture (SECR) models were used to estimate densities (Efford, 2004; Borchers & Efford, 2008)The basic parameters for this model are detection probability at home range centre g0 and spatial scale of detection function σ. The concept behind this modelling is that animals are assumed to be distributed independently in space and to occupy home ranges. The model incorporates spatial locations of captures to model detection probability g as a declining function of increasing distance (σ) from the activity/home range centre (Efford, 2004) akin to distance sampling. I analysed this data in the "secr" R package version 3.1.8(Efford, 2018).

For estimating density trend, I subset the same area sampled in 2011 and 2012 from the large sampling area of 2013 to 2016. Capture histories for tigers and leopards were recorded for both blocks separately since 2011 to 2016 and for entire Kanha national park from 2013 to 2016. Each year capture histories were converted into a multisession capture history where session represents sampling year. Multisession model of SECR was used to estimate the densities and trend across the session, i.e. finite rate of increase by fitting Session as a predictor in the model (Efford, 2018). The buffer width was decided based on the capture matrix data through suggest.buffer argument of secr 3.1.8. The minimum suggested buffer width was between 7- 8 km for both the species hence I choose 8 km buffer width around the trap array, as a model space for both tigers and leopards. The non-habitat areas (human settlements) was removed from the buffer to get the final region of model integration, i.e. habitat mask for estimating density.

Male and female sexes of these carnivores have differential home range sizes (Karanth & Nichols, 1998; Sunquist & Sunquist, 2002). Hence, sex-specific movement could be a potential cause of heterogeneity in capture probability(Efford & Mowat, 2014). I identified the gender of tigers and leopards based on secondary sexual characters from the long-term dataset. The potential source of variability was accounted by modelling g0 and σ as a function of gender, and sampling sessions as a surrogate for camera trap density.

I used hybrid mixture models of SECR (hcov argument in secr) using full likelihood approach to accommodate the unsexed individuals to gender classes based on detection and movement parameters. The mixing parameter pmix indicate and model the detection parameter to the sexes (male & female) as a two-class known mixture. The parameter pmix gives us the sex ratio as mixing proportion of the sexes. The best model was based on Akaike information criteria corrected for small samples (AICc) (Burnham and Anderson 2002). The multisession model with the Session as function to density gives the coefficient that is the rate of change on the log scale, which can be back-transformed to get the finite rate of increase(Efford, 2018). Movement parameter σ is often used as a surrogate for home range sizes (Efford et al., 2016). At landscape scale, home range as indexed by σ was shown to be density dependent as it declined exponentially with tiger densities. I test this premise at the local scale (Sadhu et al., 2017) by modelling σ as linear function of tiger and leopard density.

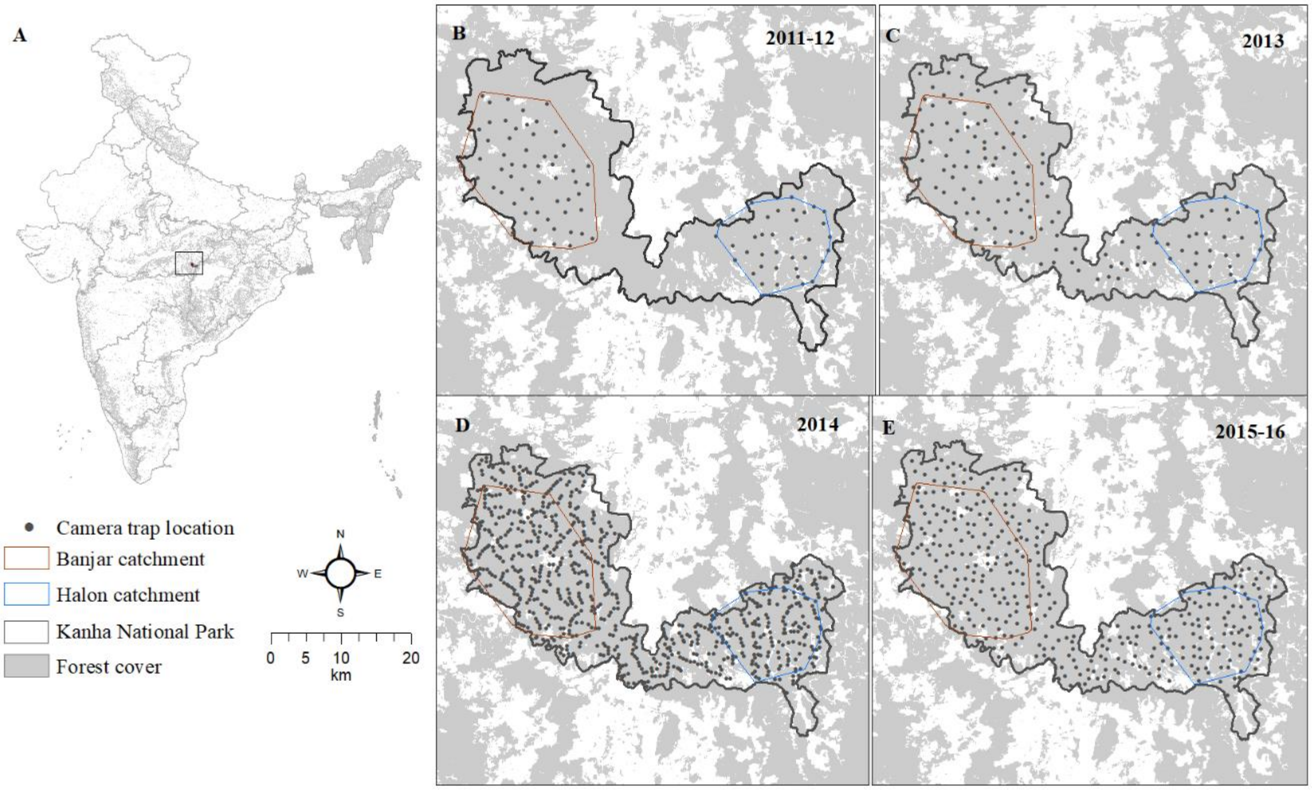

Figure 2. 1: Study design at Kanha National Park A) Map showing location of Kanha National Park in India, Sampling design (B) in 2011 & 2012, (C) in 2013, (D) in 2014, and (E) in 2015 & 2016. Data from areas that were consistently sampled across all year.

2.3 Results:

With an annual effort ranging between 3992 to 34868 trap nights, I photo-captured 125 adult tigers that included 61 males and 64 females; 217 adult leopards that included 78 males, 120 females and 19 of unknown gender. None of the individuals in the study visited both Banjar and Halon catchments within the same year, suggesting a clear separation between sites. Total annual photo-captures for tigers for the Protected area Kanha national park (PA) were between, 122 to 1584 and for leopard between, 57 to 935. The gender of all tigers and 91% of leopards were identified from the camera trap photos.

The best model for both tigers and leopards for the entire data representing Kanha national park as well as for individual blocks/catchments was the same, wherein variation in g0 and σ were explained by sex as well as sampling years (Table 2.2 & 2.3). Tiger density of Kanha PA (at 100 km^{-2}) ranged from 4.82 ± 0.33 to 5.21 ± 0.55 and the leopard densities (at 100 km^{-2}) varied between 6.63 ± 0.71 to 8.64 ± 0.75 (Table 2.2). Since variation in sex ratio between years did not contribute to explaining the data and was therefore not selected in the top model, I report the overall sex ratio for each catchment (except for leopard estimates in Banjar catchment, Table 2.2). Overall sex ratios in Kanha national park (M:F) was biased towards females for both tigers (0.66 ± 0.03) and leopards (0.50 ± 0.02).

Table 2. 1: Sampling effort, detections and population estimates of tigers and leopards within Kanha National Park, Banjar and Halon catchments within Kanha NP between 2011 to 2016. (M- male, F- female, UN- unidentified sex.) across all years.

Site	**Sampling Year**	**Camera Locations**	**Effort(Trap nights)**	**Average Trap distance**	**Tiger**			**Leopard**		
					No. detections	**Unique Tigers (M, F)**	**Population Estimate Realised ($\hat{N}$)**	**No. detections**	**Unique Leopards (M, F, UN)**	**Population Estimate Realised ($\hat{N}$)**
Banjar Catchment	2011	58	2842	1.8	314	33 (13, 20)	35 ±1.5	84	20 (9, 10, 1)	22 ± 1.66
	2012	58	2092	1.8	253	33(13, 20)	34 ± 1.3	86	21 (9, 11, 1)	24 ± 2.0
	2013	58	2610	1.8	291	41(16,25)	44 ± 1.71	100	24 (9, 12, 3)	30 ± 2.76
	2014	279	8129	0.5	965	53 (23, 30)	54 ± 0.98	129	29 (13, 16, 0)	36 ± 2.70
	2015	140	4848	1.0	686	45(19, 28)	48 ± 1.73	75	30 (23, 7, 0)	39 ± 3.34
	2016	140	6468	1.0	849	47 (23, 24)	51 ± 2.01	257	37 (17, 18, 2)	42 ± 2.43
Halon Catchment	2011	38	1368	1.8	122	10 (2,8)	10 ±0.19	61	15 (8, 7, 0)	17 ± 1.72
	2012	38	1900	1.8	192	12 (5,7)	12 ± 0.17	57	14 (8 ,6, 0)	16 ± 1.69
	2013	38	1824	1.8	121	10(5,5)	10 ± 0.13	72	16 (7, 8, 1)	19 ± 1.87
	2014	191	3831	0.5	276	14 (8,6)	14 ± 0.08	91	19 (8, 11,0)	21 ± 1.53
	2015	98	2346	1.0	165	12(8,4)	12 ± 0.09	115	25 (10, 14, 1)	27 ± 1.53
	2016	98	4280	1.0	206	9 (4,5)	09 ± 0.08	269	28 (11, 17)	29 ± 0.85
Kanha National Park	2013	155	7595	1.8	542	60 (26, 34)	61 ± 0.9	250	57 (22, 28, 7)	71 ± 4.35
	2014	758	34868	1.8	1584	74 (37, 37)	74 ± 0.48	520	84 (35, 48, 1)	91 ± 2.71
	2015	384	15360	1.8	1179	62 (27, 35)	62 ± 0.49	335	85 (41, 40, 4)	91 ± 2.49
	2016	384	18816	0.5	1477	62(27, 35)	62 ± 0.46	935	105(38,62,5)	109 ± 2.17

Table 2. 2: Model Selection Table for Kanha national park.

Site	Species	model	npar	logLik	AIC	AICc	dAICc	AICcwt
Kanha National park	Tiger	D~Session g0~h_2 σ~session + h_2 pmix~h_2	10	-10394.80	20809.60	20810.49	0.00	0.94
		D~Session g0~h_2 σ~session + h2 pmix~session + h_2	13	-10394.19	20814.38	20815.87	5.38	0.06
		D~Session g0~1 σ~session + h_2 pmix~session + h_2	12	-10421.76	20867.52	20868.79	58.30	0.00
		D~Session g0~h_2 σ~h_2 pmix~h_2	7	-10483.09	20980.17	20980.62	170.13	0.00
		D~Session g0~1 σ~h_2 pmix~h_2	6	-10511.90	21035.81	21036.14	225.65	0.00
		D~Session g0~1 σ~1 pmix~h_2	5	-10828.44	21666.88	21667.12	856.63	0.00
	Leopard	D~Session g0~h_2 σ~session + h_2 pmix~h_2	10	-5697.74	11415.49	11416.17	0.00	0.88
		D~Session g0~h_2 σ~session + h_2 pmix~session + h_2	13	-5696.51	11419.02	11420.17	4.00	0.12
		D~Session g0~1 σ~session + h_2 pmix~session + h_2	12	-5704.59	11433.18	11434.17	17.99	0.00
		D~Session g0~h_2 σ~h_2 pmix~h_2	7	-5721.64	11457.28	11457.63	41.45	0.00
		D~Session g0~1 σ~h_2 pmix~h_2	6	-5733.80	11479.60	11479.86	63.69	0.00
		D~Session g0~1 σ~1 pmix~h_2	5	-6058.24	12126.48	12126.67	710.50	0.00

npar = No. of parameters, Session= sampling session used as predictor, g0 = Detection probability at home range centre, σ = sigma Movement parameter, session = variable for each sampling year, *pmix* = Mixing proportion of two sexes, h_2 = *Sex*

Table 2. 3: Model Selection Table for Banjar & Halon catchments.

Site	Species	model	npar	logLik	AIC	AICc	dAICc	AICcwt
Banjar Catchment	Tiger	D~Session g0~ h_2 σ~session + h_2 *pmix*~h_2	12	-6183.79	12391.58	12392.89	0.00	1.00
		D~Session g0~h_2 σ~session + h_2 *pmix*~session + h_2	17	-6184.28	12402.56	12405.18	12.29	0.00
		D~Session g0~1 σ~session + h_2 *pmix*~session + h_2	16	-6219.18	12470.36	12472.67	79.78	0.00
		D~Session g0~h2 σ~h_2 *pmix*~h_2	7	-6262.95	12539.89	12540.35	147.46	0.00
		D~Session g0~1 σ~h_2 *pmix*~h_2	6	-6315.21	12642.42	12642.76	249.87	0.00
		D~Session g0~session σ~session *pmix*~h_2	15	-6376.47	12782.95	12784.98	392.09	0.00
		D~Session g0~1 σ~1 *pmix*~h_2	5	-6572.04	13154.08	13154.32	761.43	0.00
	Leopard	D~Session g0~1 σ~session + h_2 *pmix*~session + h_2	16	-1899.85	3831.70	3835.47	0.00	0.64
		D~Session g0~h_2 σ~session + h_2 *pmix*~session + h_2	17	-1899.84	3833.69	3837.96	2.49	0.18
		D~Session g0~h2 σ~session + h_2 *pmix*~h_2	12	-1905.95	3835.91	3838.01	2.54	0.18
		D~Session g0~1 σ~h_2 *pmix*~h_2	6	-1988.38	3988.76	3989.30	153.83	0.00
		D~Session g0~h_2 σ~h_2 *pmix*~h_2	7	-1987.98	3989.96	3990.69	155.22	0.00
		D~Session g0~session σ~session *pmix*~h_2	15	-2039.31	4108.62	4111.93	276.46	0.00
		D~Session g0~1 σ~1 *pmix*~h_2	5	-2150.93	4311.87	4312.26	476.78	0.00
Halon Catchment	Tiger	D~Session g0~h_2 σ~session + h_2 *pmix*~h_2	12	-2144.59	4313.18	4318.95	0.00	0.84
		D~Session g0~h_2 σ~h_2 *pmix*~h_2	7	-2153.23	4320.47	4322.37	3.41	0.15
		D~Session g0~1 σ~h_2 *pmix*~h_2	6	-2157.26	4326.52	4327.92	8.96	0.01
		D~Session g0~h_2 σ~session + h_2 *pmix*~session + h_2	17	-2141.64	4317.28	4329.77	10.82	0.00
		D~Session g0~1 σ~session + h_2 *pmix*~session + h_2	16	-2145.78	4323.57	4334.45	15.49	0.00
		D~Session g0~session σ~session *pmix*~h_2	15	-2168.98	4367.96	4377.37	58.42	0.00
		D~Session g0~1 σ~1 *pmix*~h_2	5	-2184.53	4379.05	4380.04	61.08	0.00
	Leopard	D~Session g0~h_2 σ~session + h2 *pmix*~h_2	12	-1570.91	3165.82	3168.82	0.00	0.87
		D~Session g0~1 σ~h_2 *pmix*~h_2	6	-1580.27	3172.54	3173.31	4.48	0.09
		D~Session g0~h_2 σ~h_2 *pmix*~h_2	7	-1580.09	3174.19	3175.21	6.39	0.04
		D~Session g0~1 σ~session + h_2 *pmix*~session + h_2	16	-1570.73	3173.45	3178.89	10.07	0.00
		D~Session g0~h_2 σ~session + h_2 *pmix*~session + h_2	17	-1570.14	3174.28	3180.46	11.64	0.00
		D~Session g0~session σ~session *pmix*~h_2	15	-1642.52	3315.04	3319.80	150.97	0.00
		D~Session g0~1 σ~1 *pmix*~h_2	5	-1659.81	3329.62	3330.16	161.34	0.00

Table 2. 4: Density (at 100 km-2), detection probability (g0), spatial scale of detection (σ km), and detection corrected sex ratio of tigers and leopards in Kanha national park, Halon and Banjar Catchments.

Site	Sampling Year	Tiger						Leopard					
		Density (100 km^{-2})	g_0 Female	g_0 Male	σ (km) Female	σ (km) Male	Sex Ratio (M: F)	Density (100 km^{-2})	g_0 Female	g_0 Male	σ (km) Female	σ (km) Male	Sex Ratio (M: F)
Banjar Catchment	2011	6.34 ± 0.80	0.07 ± 0.003	0.05 ± 0.001	1.59 ± 0.05	2.56 ± 0.08	0.55 ± 0.03	4.36 ± 0.76	0.003 ± 0.001	0.003 ± 0.001	1.39 ± 0.09	2.98 ± 0.2	0.45 ± 0.09
	2012	6.99 ± 0.64			1.86 ± 0.07	3.00 ± 0.10		5.30 ± 0.66			1.64 ± 0.12	2.71 ± 0.08	0.37 ± 0.08
	2013	7.70 ± 0.53			1.64 ± 0.06	2.64 ± 0.09		6.10 ± 0.57			1.30 ± 0.08	2.58 ± 0.08	0.35 ± 0.08
	2014	8.49 ± 0.54			1.41 ± 0.02	2.27 ± 0.05		7.03 ± 0.59			0.79 ± 0.04	1.66 ± 0.07	0.54 ± 0.08
	2015	9.36 ± 0.74			1.39 ± 0.03	2.25 ± 0.05		8.09 ± 0.80			0.78 ± 0.05	1.68 ± 0.09	1.86 ± 0.09
	2016	10.32 ±1.09			1.27 ± 0.03	2.04 ± 0.04		9.30 ± 1.26			1.04 ± 0.04	2.23 ± 0.08	0.54 ± 0.07
Halon Catchment	2011	2.27 ± 0.50	0.05 ± 0.003	0.04 ± 0.003	2.64 ± 0.16	3.74 ± 0.28	0.66 ± 0.06	4.98 ± 0.97	0.04 ± 0.004	0.03 ± 0.002	1.21 ± 0.11	2.48 ± 0.20	0.46 ± 0.04
	2012	2.24 ± 0.37			2.30 ± 0.12	3.25 ± 0.23		5.32 ± 0.80			1.23 ± 0.12	2.54 ± 0.21	
	2013	2.21 ± 0.29			2.46 ± 0.15	3.58 ± 0.23		6.00 ± 0.67			1.17 ± 0.09	2.41 ± 0.20	
	2014	2.19 ± 0.29			2.21 ± 0.89	3.13 ± 0.14		6.59 ± 0.64			1.05 ± 0.08	2.16 ± 0.20	
	2015	2.16 ± 0.36			2.40 ± 0.16	3.39 ± 0.19		7.24 ± 0.82			1.01 ± 0.06	2.08 ± 0.13	
	2016	2.13 ± 0.47			2.08 ± 0.87	2.95 ± 0.13		7.95 ± 1.19			1.34 ± 0.07	2.76 ± 0.13	
Kanha National Park	2013	5.21 ± 0.55	0.04 ±0.001	0.03 ± 0.0008	2.60 ± 0.50	3.03 ± 0.75	0.66 ± 0.03	6.63 ± 0.71	0.018 ± 0.001	0.02 ± 0.001	1.40 ± 0.06	2.52 ± 0.09	0.50 ± 0.02
	2014	5.01 ± 0.34			1.59 ± 0.23	2.37 ± 0.45		7.24 ± 0.49			1.34 ± 0.04	2.44 ± 0.06	
	2015	4.87 ± 0.33			1.95 ± 0.35	2.91 ± 0.52		7.90 ± 0.46			1.59 ± 0.63	2.86 ± 0.08	
	2016	4.82 ± 0.33			1.85 ± 0.30	2.76 ± 0.44		8.64 ± 0.75			1.84 ± 0.50	2.92 ± 0.07	

The density for both tigers and leopards in Banjar catchment showed growth with a $\lambda = 1.10$ ($CI_{95\%}$ 1.08-1.18) for tigers and $\lambda = 1.15$, ($CI_{95\%}$ 1.05-1.27) for leopards (Table 2). While for the Halon catchment tiger and leopard density remained stable at $\lambda = 0.98$ ($CI_{95\%}$ 0.86-1.14) and $\lambda = 1.09$ ($CI_{95\%}$ 0.98-1.22) respectively (Table 2.4, Figure 2.2).

Average σ, the scale parameter estimated by SECR, which is an index of home-range size, showed a declining trend with increasing density for both genders of both tigers (♂, r= -0.93 & ♀, r= -0.94; P<0.001) and leopards (♂= r -0.56, P=0.056; ♀= r -0.57, P=0.05) (Fig 2.3).

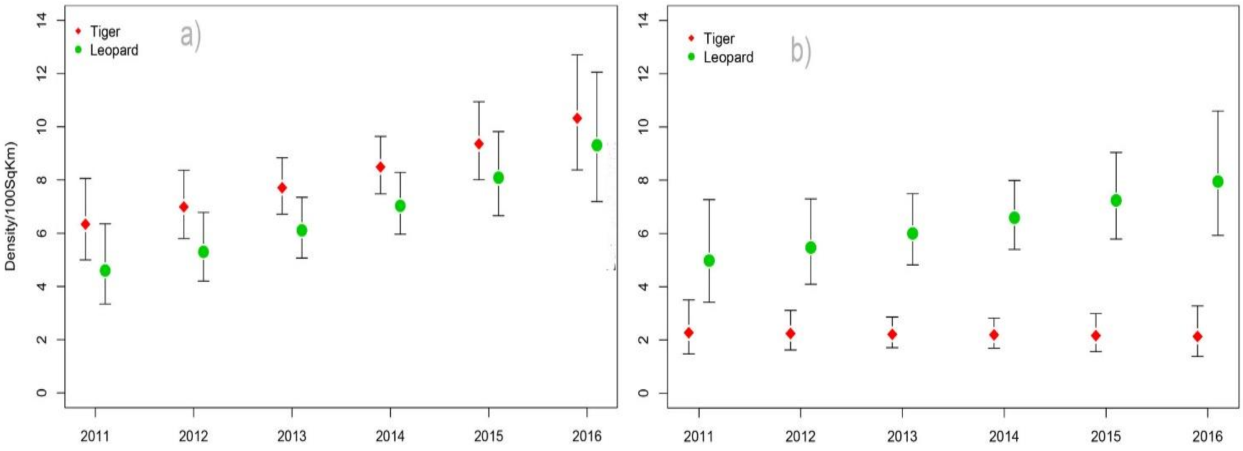

Figure 2. 2: Trend in tiger and leopard densities (a) Banjar catchment (b) Halon catchment, consistently sampled across all six years at Kanha national park.

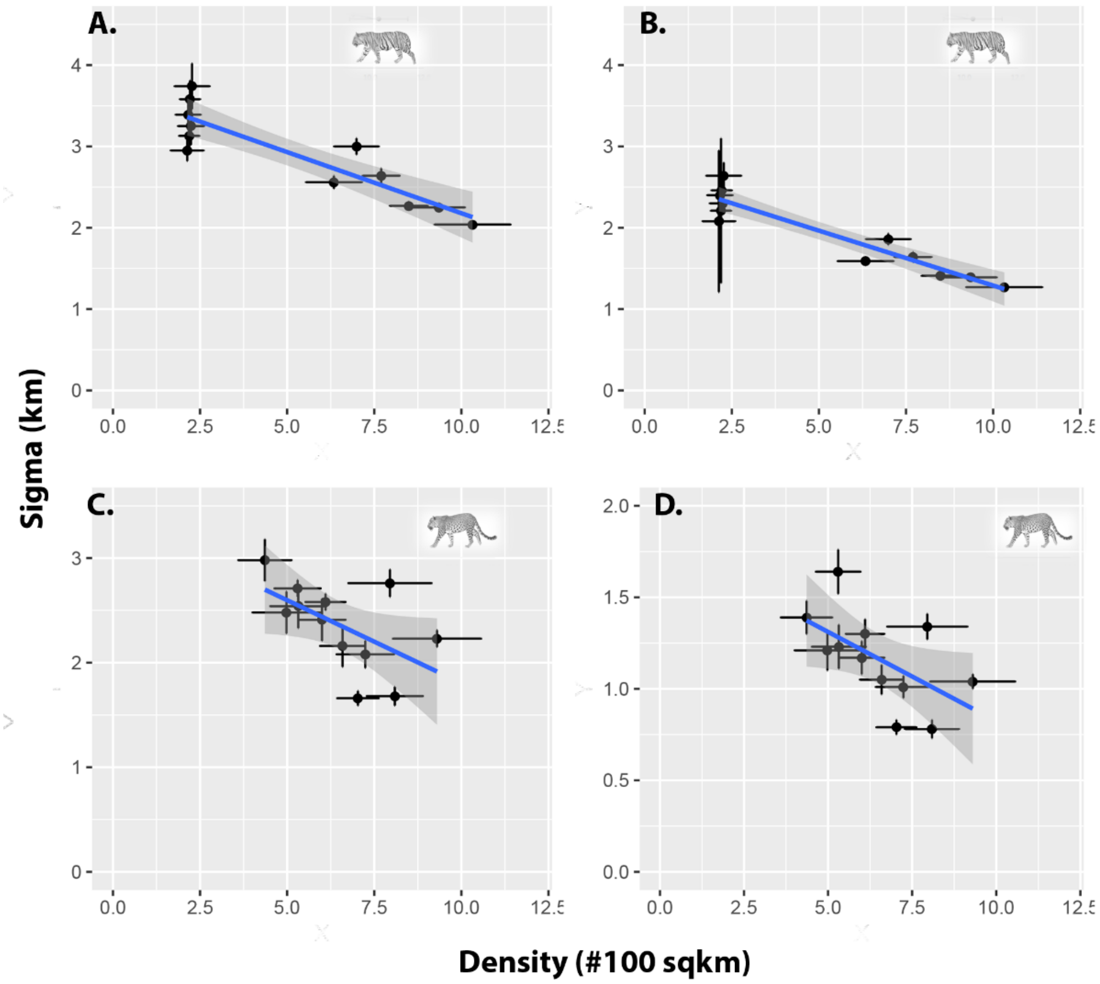

Figure 2. 3: Relationship between Sigma σ (km ± SE), an index of home-range vs Density (at 100 km-2 ± SE), A) female tigers, B) male tigers, C) female leopards and D) male leopards.

2.4 Discussion:

The overall density of tigers and leopards in Kanha National Park did not show any trend (Table 2.4, Figure 2.2). The density of leopards was significantly higher than the tigers. The two sampling blocks, Banjar and Halon catchments, were selected based on substantial differences in prey densities and conservation investments with the objective of studying the response of large carnivores to these differences. Contrary to expectation, both predators occurred at reasonably high densities and both showed positive growth in the Banjar catchment. Here, tigers density (at 100 km^{-2}) significantly increased from 6.34 to 10.32, while leopards density (at 100 km^{-2}) increased from 4.36 to 9.30 (Table 2.1). While in Halon catchment that had fewer prey and less investment in conservation management, both carnivores did not show a detectable increase. Tigers are more K-selected when compared to leopards (Chapron et al., 2008) and should exhibit slower life history traits manifesting in slower population growth when compared to leopards. But contrary to expectations, the growth rate of leopards was comparable to that observed for tigers. This result is suggestive of competitive inhibition of leopards by the larger tiger. Besides competing for food (which was plentiful), tigers are known to pursue and kill leopards (McDougal ,C. , 1988). Leopard densities were significantly higher compared to tiger densities in Halon catchment and both carnivore populations did not show growth here. I believe that this was a due to high human disturbance and possibly poaching of prey and carnivores. Leopards fare better than the tiger in face of poaching due to higher illegal demand for tiger body parts, as well as by having faster life history traits compared to tigers (Chapron et al., 2008). This was reflected in Halon catchment that had more leopards compared to tigers. Efford et al. (2016) showed an exponential decline in σ with increasing tiger density at landscape scales. Density dependent home range sizes have been published for many species (Trewhella, Harris, & McAllister, 1988; Hoset et al., 2007; Sadhu et al., 2017). These suggest that home-range size adjusts like an elastic disk to changes in density (Krebs J. R., 1971) and when nearing carrying capacity the rate of decrease in home-range size is no longer possible (reaches an asymptote). The local scale data for σ of both tigers and leopards showed a linear decline with density suggesting that the population of both tigers and leopards was not yet at carrying capacity and could potentially increase further.

Earlier traditional estimates using non-spatial CMR as well as most SECR rarely take into account local variations in density, and population well-being is inferred from the overall response in density and its trends for the PA. This could mislead policy and management decisions (Gaston, Blackburn, & Gregory, 1999). This study highlights the importance of estimating densities at local as well as PA scale since diverse responses to differential management and prey populations are possible within the same PA and inference from any one area or from the entire PA could be misleading. The low-density area of Halon catchment would benefit substantially by an increased protection regime and reduction of human disturbance. SECR when employed in a proper study design provides result required for site-specific management of endangered species populations.

CHAPTER 3. DEMOGRAPHY OF TIGERS

3.1 Introduction:

Knowledge of key vital rates such as reproductive parameters and survival rates are important for developing effective recovery strategies for the endangered species (Johnson et al., 2010). However, such information is rare due to elusive nature, low density and methodological challenges for assessing carnivore populations. Seventy percent of surviving wild tigers are in the Protected Areas (PA's) constituted by 07% of remaining tiger habitat (Walston et al., 2010). These PAs acts as source sites, which support breeding populations. Long-term viability of source populations is important to repopulate the larger landscape. Waltson et al. (2010) identified 42-source site of tigers worldwide, Kanha tiger reserve in India is one of them. Kanha tiger reserve is a global tiger priority landscape of level I category and acts as a major source site for tigers in central Indian forests (Wikramanayake et al., 2011).Tigers are globally declining due to habitat loss, prey depletion and demand driven poaching (Walston et al., 2010, Wikramanayake et al., 2011). The connectivity between tiger source sites are important in the metapopulation framework in central India for long term persistence, as none of the PAs have more than 100 tigers.

Studies on tiger demography are scarce. The pioneering work of Smith & McDougal, (1991) that used radio-telemetry on tigers, Kerley et al., (2003),and Sadhu et al., (2017) were the best source of information on reproductive parameters and survival probabilities. Limitation of sample size was a major concern for the telemetry-based studies. Karanth et al., (2006), Duangchantrasiri et al., (2016), and Bisht et al., (2019) used camera trap based Capture Mark Recapture(CMR) based study to address this sample size limitation. However, the camera trap based CMR study cannot distinguish between permanent emigration and mortalities (Pollock, 1982). Recent development of open spatially explicit capture recapture models addresses the emigration by modelling dispersal movement parameters (Ergon & Gardner, 2014, Gardner et al., 2018) but this required large-scale camera trapping to capture sufficient dispersal events within the sampling state space. Tigers are known to disperse several kilometres (more than 100 km) from their natal areas hence delineating state space for dispersal is difficult and requires high level of investment and subsequent computational effort.

In this chapter, I present my study on the demography of tigers in the PA of Kanha tiger reserve with known fate and CMR based models to separate the mortality and emigration from apparent survival.

3.2 Methods:

Field method for known fate survival:

I collated data from 127 tigers, those were regularly monitored since Jan 2005 to July 2018. The intensive study area was primarily the tourism zone of the tiger reserve. Regular monitoring of tigers as done by forest staff and researchers on elephant back, routine foot patrolling by trackers, radio-telemetry, tourist photography, and through camera traps. Thirteen tigers were radio-collared between 2005 to 2014 under the long-term tiger-monitoring project in Kanha tiger reserve. Each tiger was identified either through its pelage pattern or through VHF frequency of it’s collar. A monitoring register was maintained on tiger sightings by the park management with photographs taken by park visitors and management staff. Kanha receives around 1.2 lakh visitors annually many of them being ardent wildlife photographers. Most of the visitors willingly contributed information on tiger sightings along with photographs.

Robust design Camera trapping:

I used multi-year camera trap based capture-mark-recapture (CMR) framework in a robust design framework to estimate apparent survival probabilities and annual abundance. Initially, due to limited logistic, I sampled the survey area in two blocks with a total area of 460 km^2. Later with the increase in resources, I gradually increased the sampling area in subsequent years (Table 3.1). Since 2013 onwards, the entire National Park was sampled with camera traps. With the extra resources, the camera densities were subsequently increased from 2014 to gain better precision on the estimates (Table 3.1). Camera trap locations were selected to maximise photo captures after extensive sign surveys on forest roads, trails and streambeds (Figure 3.1).

Data preparation and Analysis

For Known Fate:

I used known-fate (KF) model (Kaplan–Meier estimator) in program Mark 8.1 (Cooch & White, 2011) to estimate the stage and sex specific annual and span survival of tigers. This KF model estimate survival if the fate of the individual known with certainty and independently during the period of monitoring (Williams, Nichols, & Conroy, 2002). Since not all the individuals may enter the study concomitantly, they were added in a staggered entry (Pollock et al., 1989, Subedi et al., 2017, Sadhu et al., 2017). I used the age categories (six categories) developed by Sadhu et al. (2017) for classifying the age-stage of tigers. These were juvenile (1-2 year), sub-adult (2-3 year), young adult (>3-5year), prime adult (5-10 year) and old adult (>10 years). I pooled the detections into a 06 and 03 months intervals for the adults (>1 year of age) and cubs respectively as these time intervals were meaningful for estimating survival for long lived adult tigers and for cubs as well as practical for getting observations for each individuals within this period (Sadhu et al 2017). The fate of individuals as dead or alive was recorded during these intervals. I censored an individual from the analysis for periods it was not detected but subsequently detected (Williams, Nichols, & Conroy, 2002).The survival of adults and cubs were analysed separately. It was not always possible to sex all the cubs, during the initial months and at that age, mortality was unlikely to be gender specific. Therefore, all cubs (males and females) were pooled for a single estimate of survival.

A live-dead-censored matrix was prepared for each individual’s fate, 10 was classified as surviving an interval, 11 as dead during that interval and 00 classified as censored during a particular interval (Cooch and White, 2009). The full model in Mark for adult tigers (>1years) had sex and five stages. Various combinations of this full model were tested using Akaike Information Criteria corrected for sample size (AICc) to select the best model that explained the observed data. To account for model uncertainty (Burnham & Anderson, 2002), I used AICc weighted model averaging for parameter estimates.

For Robust design:

The CMR based classical open population models in which population was open to demographic process (recruitment, deaths, immigration and emigration) during the study were used to study population dynamics and estimate parameters such as apparent survival (Williams, Nichols, & Conroy, 2002). The Pollock robust design model originally developed by Pollock, (1982) and later refined by Kendall & Bjorkland, (2001) is two step model within one analysis where sampling occurred at two temporal scales; the primary and secondary periods. The primary period is a longer interval and the population is considered open between two primary periods. Each primary period is made up of secondary periods that are of shorter duration and the population is assumed to be closed within this secondary period (Otis et al., 1978).

In PRD model the transitional probabilities between being available or not for capture (temporary emigration), during each primary period is accounted for. Here, each year of the seven years of camera trap sampling was considered as a primary period, while the sampling duration in each year (41 to 50 days) were the secondary periods (Table 3.1).

I identified individual tigers from camera trap images across seven years of the sampling since 2011-2017 by using Extract Compare a pattern recognition software developed exclusively for tiger stripe pattern (Hiby et al., 2009). Capture matrix of individual tigers were prepared in the standard X matrix format (Otis et al., 1978). I identified the gender of each individual tiger with help of the long-term database from their genitals and secondary sexual characters (nipples). For this analysis only adult individuals (>1 years of age) were included for estimating survival probability, since cubs have high mortality and low detection probability by camera traps (Karanth, 1995). Age-stage specific survival estimation was also not possible because it is not always possible to differentiate between adult age-stages from camera-trap pictures (Sadhu et al., 2017)which usually requires good photos of tiger dentition. Therefore, single estimates of gender specific (all age groups >1 year) survival was obtained.

Data were analysed in Program Mark version 8.1 (Cooch & White, 2011), with Huggins robust design data type. The Huggins based analysis is a conditional likelihood models where individual covariates such as 'sex' can be used to model survival and detection while abundance is a derived parameter. I estimated sex specific survival probabilities (φ), temporary emigration probabilities (γ', γ''), capture probability ($\boldsymbol{p}$) and recapture probabilities ($\boldsymbol{c}$) using Huggins conditional likelihood based models in PRD framework.

Detection model:

I first built detection models of individual tigers by using capture-recapture histories within each primary period. Since, tiger do have sex specific movement/home ranges like other solitary carnivores, sex specific heterogeneity in detections model was expected and tested by AICc. The change in camera trap spacing between years could also be a potential source of variability in detections. Kanha tiger reserve received substantially high rainfall during 2015 when the sampling was ongoing. Due to rainfall many traps missed detections, hence, I accounted for this source of variability in detection by modelling such period (year) as a covariate.

The full detection model was {$\boldsymbol{p}$ (male [2011-2013, 2014, 2015, 2016-17], female [2011-2013, 2014, 2015, 2016-17]) $\boldsymbol{c}$ (male [2011-2013, 2014, 2015, 2016], female [2011-2013, 2014, 2015, 2016])}. Capture probability ($\boldsymbol{p}$) and recapture probability ($\boldsymbol{c}$) potentially varied due to sex and sampling intensities. I did not account for individual heterogeneity within the sexes due to limited sample size, as these models were complex and failed to converge.

Transition model: The state and transition parameters survival probabilities (φ) and temporary emigration & immigration probabilities (γ,' γ'') respectively were modelled by using the model that best described the detection process. I assume that the φ, γ,' and γ'' will not change between years due to similar protection regime and conservation investments across the years. However, sex specific variation in φ, $\boldsymbol{\gamma'}$**,** and $\boldsymbol{\gamma''}$ are expected as in carnivores males disperse more often and farther and therefore face more risks to their life while females are mostly philopatric and likely have higher survival probabilities (Smith 1998). If γ'**,** and γ'' were consistently estimated to be very small (<0.001) I fixed them at zero for parsimony in subsequent models.

I fitted 12 models with several combinations of parameters as stated above for the PRD analysis. I used sample size corrected Akiake's information criteria (AICc) (Akiake 2011) for selecting the model that best explained my data. Model averaging (for less than 10 dAICc) was done to account for uncertainty in model selection(Burnham & Anderson, 2002).

Recruitment rate:

Since the sampling area was constant from 2013 to 2017 hence 5 years of data was used to estimate recruitment rate. Here I consider recruitment of adult individuals (>1 years old tigers) which were added to the population either by attaining age of >1 year or through immigration from neighbouring areas. I estimated number of recruits (**B***ₜ*) in time ***t*** as;

$\mathbf{B}_t = \widehat{N}_{t+1} - \widehat{N}_t \times \varphi$ where; $\widehat{N}_{t+1}$ = Population estimate at time t+1, $\widehat{N}_t$ = Population estimate t, φ = Survival probability(Skalski, Ryding, & Millspaugh, 2005). Average recruitment rate was estimated for Kanha national park across the 2013 to 2017.

Population Turnover rate:

Population turnover rate from 2013 to 2017 was estimated as proportion of individuals changing between years.

Female reproductive parameters:

The parturient and lactating females were restrictive in their movement but frequently detected through regular elephant monitoring and camera trapping. Birth of cubs were confirmed by direct sighting by experienced mahouts and research team or photo-captured either through camera traps or by hand held photography done by tourists who shared their photographs with information on date and location. The detection of mother with cubs of age < 02 months was rare; hence, litter size estimates may be negatively biased as mortality under two months was not recorded (Sadhu et al., 2017). The age of first reproduction and inter-birth interval were recorded by continuous monitoring either through radio-telemetry or through elephant based monitoring of individually known tigress. For computing estimates of these parameters I used only those tigresses and intervals for which I was reasonably certain of not missing births as the status of these tigresses were recorded several times each month in the preceding and intervening periods. Reproductive rate of female was estimated using average litter size /average Inter birth interval (years) (Wielgus & Bunnell, 1994).

Full udders in a tigress are visible about a week prior to parturition and lactation lasts for about 155 days in tigers (Bisht et al., 2019). Thus, a tigress near term and with cubs can be ascertained from the status of her teats and udders for about 165 days. For estimating numbers of (detection corrected) breeding females per year, all females that delivered cubs of <5 months before the sampling period would be the part of the pool of breeding females available for each sampling year. Identification of breeding female (pregnant and lactating) from CMR data was done on the basis of visual examination of full udders and teats in the camera trap pictures of tigers (Sadhu et al., 2017). Following formula was used to calculate the number of breeding female per year (Bisht et al 2019).

Breeding female per year = $(\frac{\mathrm{N_{Bf}}}{\mathrm{p_f}}) \times (\frac{\mathrm{Dyear}}{\mathrm{SDyear}}) \times (\frac{\mathrm{D(bd)}}{\mathrm{SDyear}})$

$\mathrm{N_{Bf}}$ = No of breeding female photo-captured in each year, $\mathrm{p_f}$ = Detection probability of breeding female, Dyear= Days in a year (365 days), SDyear = Sampling duration (days) in each year, D(bd)= Period of breeding status detectability (165 days).

Proportion of breeding females was estimated for Kanha national park between 2013 to 2017 as the entire National Park was sampled consistently for these years.

Dispersal probability:

Survival estimates using PRD are in reality apparent survival i.e. a combined estimate of mortality and emigration. These two parameters cannot be teased apart unless spatially explicit CMR open population models is used over vast areas of the landscape (covering potential dispersal distances) (Gardner et al., 2018). While known fate analysis permits the estimate of actual survival. Since I had estimates of actual adult gender specific survival from the same population contemporaneously with apparent survival obtained by PRD, I could estimate emigration (dispersal) for each gender in adult tigers.

I estimated dispersal probability (true emigration)(D_p) for each gender

$$D_p = (\text{PRD mortality} - \text{KF mortality})$$

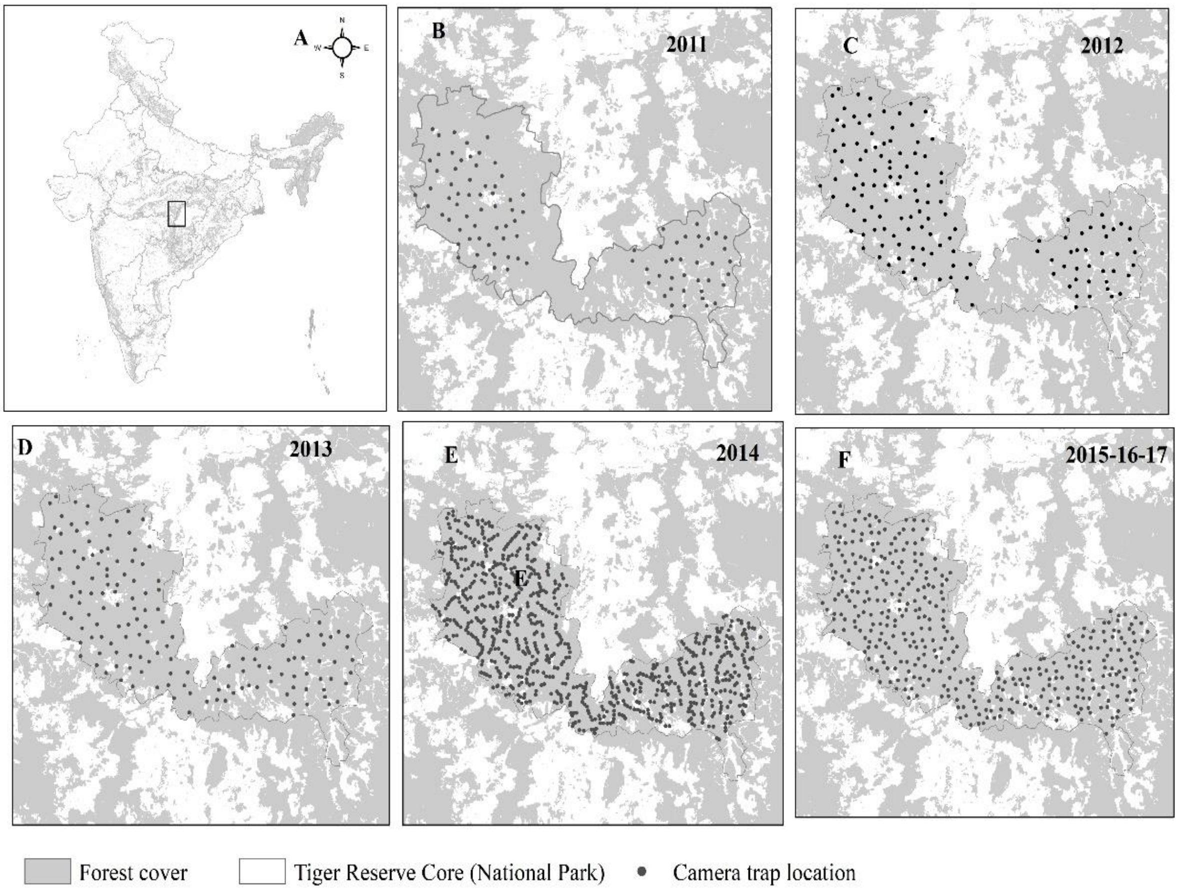

Figure 3.1: Camera trap locations in Kanha National Park between 2011 to 2017.

Table 3.1: Capture-Mark-Recapture based sampling effort and abundance estimates of tigers within Kanha National Park between 2011-2017.

Sampling Year	**Camera Locations**	**Sampling area (km^2)**	**Average Trap distance (km ± SE)**	**Duration of sampling period (secondary period (no of days)**	**Unique Individual (M_t+1)**		**Estimated population through Robust Design**	
					Males	**Females (Breeding Female)***	**Male (± SE)**	**Female (± SE)**
2011	96	460	1.74 ± 0.039	50	14	29 (5)	14 (± 0.17)	29 (± 0.10)
2012	127	660	1.77 ± 0.005	50	19	30 (6)	19 (± 0.20)	30 (± 0.10)
2013	155	916	1.73 ± 0.032	49	26	34 (7)	26 (± 0.25)	34 (± 0.12)
2014	758	916	0.52 ± 0.005	46	37	37 (8)	37(± 0.30)	37(± 0.09)
2015	384	916	1.05 ± 0.012	40	27	35 (8)	27(± 0.32)	35(± 0.47)
2016	384	916	1.05 ± 0.012	49	27	35 (7)	27(± 0.13)	35(± 0.09)
2017	389	916	1.03 ± 0.013	41	38	37 (9)	38(± 0.30)	37(± 0.18)

2.1* No of breeding females from amongst the total females, SE standard Error

3.3 Results:

Reproductive parameters:

I recorded litter size from 31 litters of 16 females. The average litter size was 3.24 (± 0.63, range 2 to 4), mother with single cub in a litter was not be recorded (Fig 3.2). I could determine the age of first reproduction for 11 tigress since they were observed continuously from the age of being cubs. Since I did not observed parturition, cubs were aged to the month and an approximate month of birth was determined (Table 3.2 & 3.3).The average age of first reproduction was 3.30 (± 0.13, range 2.67 to 4.00) years (Table 3.3). I could record 29 inter-birth intervals (IBI) from the continuous monitoring data of 15 tigress (Table 3.2). The average IBI was 22 (± 2.7, range 8 to 40) months, the shortest IBI was recorded to be 8 months. This tigress lost complete litter within one month of delivery due infanticide and came into oestrous again within 3-4 months. The tigresses at Kanha did not show any breeding season however, the majority of litters were born in winter (October - February) (Figure 3.3).The reproductive rate of female was reported to be 1.79 (± 0.09) cubs female^{-1} year^{-1}. Considering the life span of breeding female to be 12 years (Smith & McDougal, 1991), the average lifetime contribution of each female to the adult population is 10 (± 0.3) tigers.

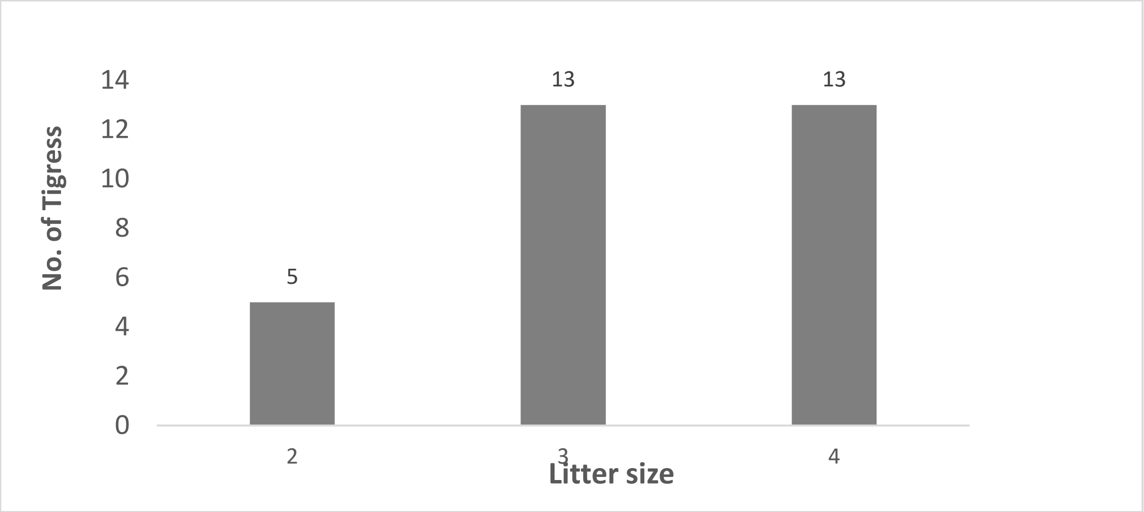

Figure 3. 2: Litter size of regularly monitored tigress in Kanha National Park

Table 3. 1: Inter-birth intervals of known tigresses (n=15) in Kanha National Park.

Sl No.	Tiger id	Litter-1	Litter-2	Litter-3	Litter-4
1	KT11	Oct-2011	Nov-2013	Nov-2015	Not recorded
2	K11	Dec-2012	Jan-2014	Aug-2015	Not recorded
3	M6	Dec-2009	Dec-2011	Jun-2014	Jan-2016
4	KT15	Oct-2009	Nov-2011	Apr-2014	Not recorded
5	KT6	Oct-2011	Jan-2013	Jul-2014	Not recorded
6	K2	Jun-2010	Sep-2012	Not recorded	Not recorded
7	K4	Apr-2011	Jan-2014	Jul-2015	Dec-2016
8	K14	Aug-2013	Aug-2015	Feb-2017	Not recorded
9	K11C	Jan-2015	Dec-2016	Not recorded	Not recorded
10	KT16	Jan-2013	Apr-2014	May-2016	Jan-2017
11	M2	Nov-2011	Feb-2013	Dec-2013	Not recorded
12	M4	Sep-2012	Jan-2016	Not recorded	Not recorded
13	ST5	Nov-2011	Sep-2012	Sep-2014	Oct-2016
14	KB1	Dec-2013	Dec-2016	Not recorded	Not recorded
15	K4A	Jul-2015	Jan-2017	Not recorded	Not recorded

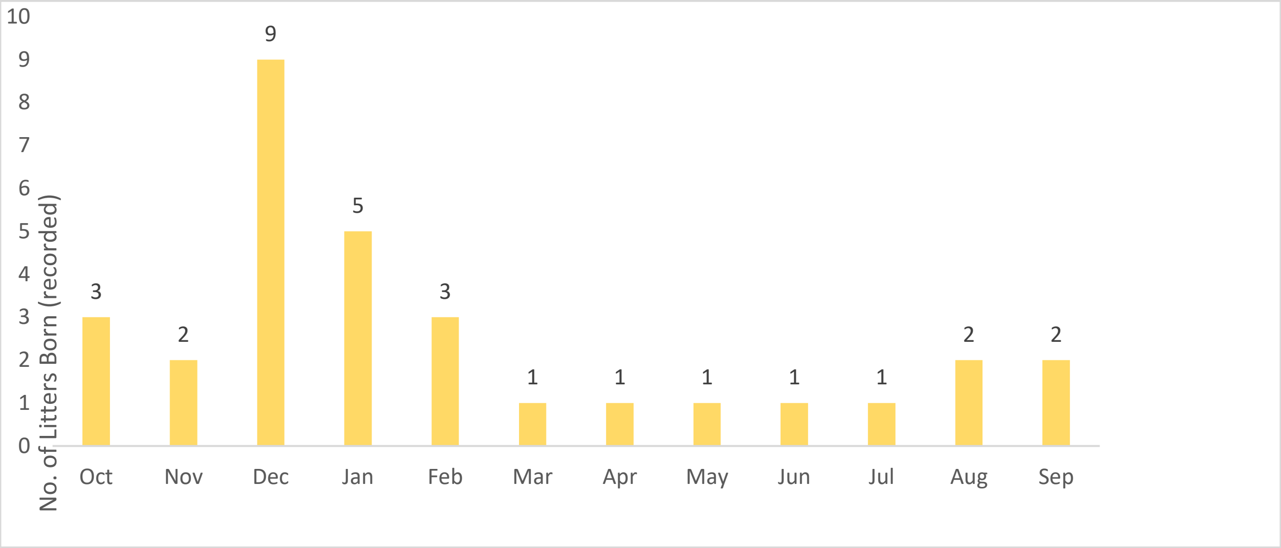

Figure 3. 3: No. of tiger litters (n=31) born during the months in Kanha National park.

Table 3. 2: Birth and first parturition records of continuously monitored tigress (n=11) in Kanha National park.

Sl No.	Tigress	Born	Parturition
1	K11C	Dec-2011	Feb-2015
2	KT6B	Jan-2013	Jan-2016
3	KT6D	Jan-2013	Jan-2016
4	M6C	Dec-2011	Dec-2015
5	KT11	Jul-2008	Nov-2011
6	KT8N2	Jan-2014	Sep-2016
7	KB1F	Dec-2009	Dec-2013
8	K4N1	Jan-2014	Jan-2017
9	KT11A	Nov-2011	Dec-2014
10	KT11N2	Dec-2013	Jul-2017
11	K11N1	Jan-2014	Jul-2017

Breeding female per year:

After correcting for detection probability and accounting of detection in each primary period 44 to 53 % of females were estimated to be breeding during each sampling session. During a year, 48.5 % (± 1.5) of the females were found to be breeding females with an average of 17 (± 0.70) females in each year within the Kanha national Park.

Known fate survival estimates:

Constant survival with no time effect was the top model for cubs survival (Table 3.4). The average annual survival rate of cubs ($\varphi_{\text{cubs}} = 0.59 \pm 0.06$) were lower than the other adult age classes (>1 year of age) (Table 5). Among Adult age classes (>1 year of age), model that consider similar survival between juveniles and sub-adults along with similar survival between young and prime adults best explained my data. However, there was high model uncertainty as several models had nearly identical AICc values and therefore model-averaged estimates were reported (Table 3.4). Female showed higher survival throughout their adult stages however, it was statistically not different from male survival estimates (Table 3.5). Male tigers exhibited a typical Type II survivorship curve while survivorship of tigresses was a curve between Type I & II (Figure 3.4).

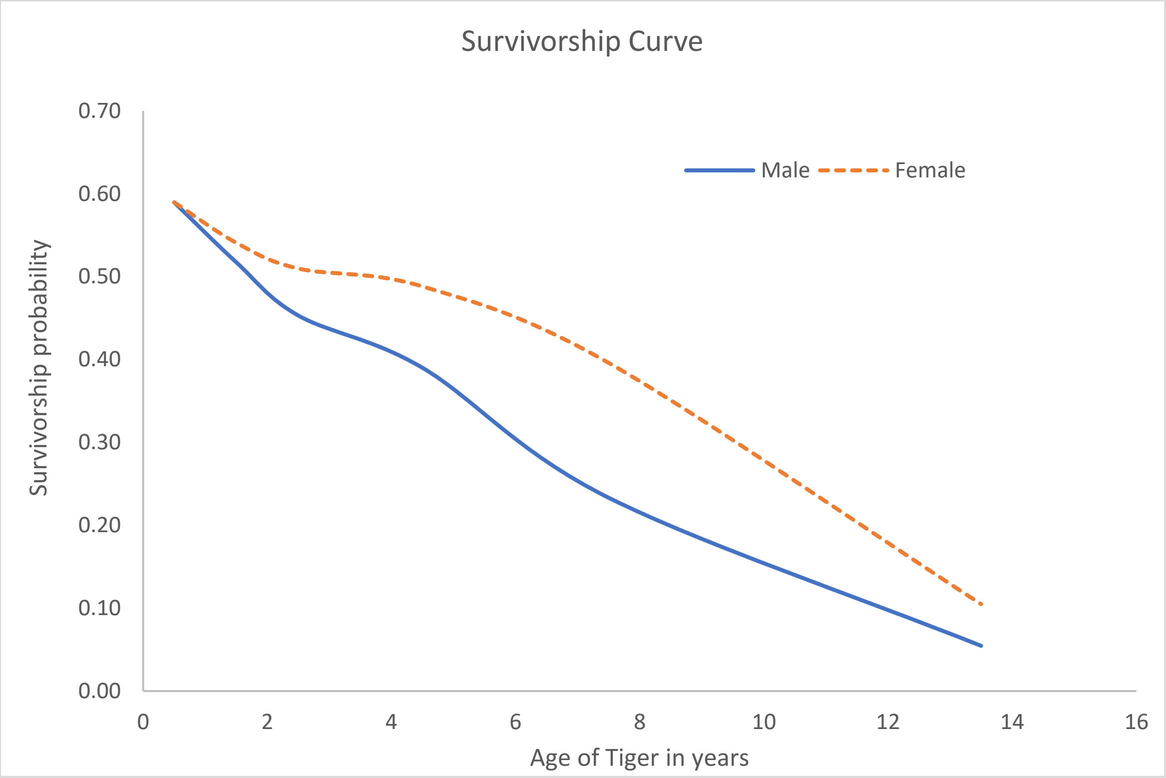

Figure 3. 4: Survivorship (cumulative survival) of Tigers in Kanha National Park, estimated from 127 tigers monitored between 2005 and 2018.

Table 3. 3: Model selection parameters for estimating survival of 127 tigers from Kanha National Park between 2011-2017 using known fate model in program MARK. Survival in subsequent stages was considered independently of earlier stage and an individual tiger was added to subsequent stages.

Age class	Sl no.	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance	-2log(L)
Cubs	1	**φ**{.}	147.23	0.00	0.93	1.00	1	1.01	145.21
	2	**φ**{*time*}	152.41	5.18	0.07	0.08	4	0.00	144.20
Adults	1	**φ**{ Female(JV=SA),Male(JV=SA),Female(YA=PA), Male(YA=PA), Female (OA) Male (OA)}	269.02	0.00	0.30	1.00	6	139.86	269.02
	2	**φ**{Sex(.) (JV,SA,YA,PA,OA)}	269.29	0.26	0.26	0.88	5	142.16	269.29
	3	**φ**{Female(SA), Male(SA), Female(YA=PA) Male(YA=PA), JV, OA}	269.79	0.76	0.21	0.68	6	140.62	269.79
	4	**φ**{Female(JV,SA,YA,PA,OA),Male(JV,SA,YA,PA,OA)}	271.10	2.07	0.11	0.35	10	133.75	271.10
	5	**φ**{JV, Female(SA),Male(SA), Female (YA=PA),Male (YA=PA), Female(OA) Male(OA) }	271.77	2.75	0.08	0.25	7	140.57	271.77
	6	**φ**{Female(JV), Male(JV) ,Female(SA),Male(SA),Female(YA=PA),Male(YA=PA), Female(OA)Male(OA)}	273.04	4.01	0.04	0.13	8	139.79	273.04
	7	**φ**{Sex(.) Stage (.)}	277.64	8.62	0.00	0.01	2	156.58	277.64
	8	**φ**{Female(JV=SA)s Male(JV=SA), Female(YA=PA=OA)Male(YA=PA=OA)}	281.25	12.22	0.00	0.00	4	156.15	281.25
	9	**φ**{sex(.) (JV,SA), (YA=PA=OA) }	282.20	13.18	0.00	0.00	3	159.12	282.20

(JV = Juveniles (1-2 years) , SA = Sub Adults (2-3 years), YA = Young Adult (3-5 years),PA= Prime Adult (5-10 years), OA = Old Adult (>10 years); time – for cub survival was 3 a month interval;)

Table 3. 4: Stage specific survival probabilities of tigers in Kanha National Park, estimated from individually known 127 tigers monitored between 2005 and 2018.

Age class	**Gender**	**Sample size**	**Average Annual survival rate (range $CI_{95\%}$)**
Cubs (< 12 months)	NA	68	0.59 (0.46- 0.70)
Juveniles ((1–2 years)	Male	12	0.88(0.65 -0.96)
	Female	17	0.92 (0.71 - 0.98)
Sub Adult (2-3 years)	Male	14	0.88 (0.63 -0.97)
	Female	20	0.94 (0.75- 0.99)
Young Adults (3-5 years)	Male	15	0.93 (0.75- 0.98)
	Female	23	0.98 (0.91- 1.00)
Prime Adults (5-10 years)	Male	19	0.90 (0.81 – 0.95)
	Female	28	0.96 (0.86 – 0.99)
Old Adult (10 and above)	Male	4	0.77 (0.47 - 0.92)
	Female	17	0.80 (0.67 - 0.88)
All Adult age class	**Male**	**64**	**0.87(0.69 - 0.95)**
	Female	**105**	**0.92 (0.80 - 0.97)**

Robust Design based vital rates:

A total sampling effort of 103738 camera trap nights provided 6959 usable photographic captures of 147 individual tigers (77 males and 70 females) during 07 years of the study (2011-2017). The detection model was best explained by the effect of gender, trap spacing and period of rainfall on capture and recapture probabilities. The transition probabilities (φ, γ' and γ'') which were parameterised on the best detection model, was explained by gender specific variation (Table 3.6). The point estimates of apparent survival of females was higher than males as expected (Table 3.7) but their 95% confidence interval overlaps. Population turnover rate was estimated to be 40 (SE 11) % and 13(SE 4.5) % for male and female tigers respectively.

Recruitment Rate:

The average recruitment rate was 9.4 (± 4.5) and 6.39 (± 1.01) individuals per year for male and female tigers respectively.

Dispersal rate:

Dispersal probability was estimated to be 09 (02-09) % for males and 08 (03-09) % for the females tigers.

Table 3. 5: Model selection parameters for estimating abundance and survival of 147 photo-captured tigers in Kanha National Park between 2011-2017 using Pollock’s robust design in program MARK.

Model Type	**Sl. No.**	**Model**	**AICc**	**Delta AICc**	**AICc Weights**	**Model Likelihood**	**Num. Par**	**Deviance**	**-2log(L)**
Transition Models	1	{ *φ* (sex), *γ*’(M,F=0), *γ*”(sex), *p*(sex,S1-S3,S4, S5,S6-S7), *c*(sex, S1-S3,S4,S5,S6-S7)}	20837.34	0.00	0.23	1.00	21	21680.67	20795.13
	2	{ *φ* (sex), *γ*’ (.), *γ*”(.), *p*(sex,S1-S3,S4, S5,S6-S7), *c*(sex,S1-S3,S4,S5,S6-S7)}	20837.36	0.02	0.23	0.99	20	21682.71	20797.17
	3	{ *φ* (.),*γ*’ (sex), *γ*” (sex), *p*(sex,S1-S3,S4, S5,S6-S7), *c*(sex, S1-S3,S4,S5,S6-S7)}	20837.82	0.48	0.18	0.79	21	21681.16	20795.62
	4	{ *φ* (sex), *γ*’ (.),*γ*” (sex), *p*(sex,S1-S3,S4, S5,S6-S7), *c*(sex, S1-S3,S4,S5,S6-S7)}	20838.30	0.96	0.14	0.62	21	21681.63	20796.09
	5	{ *φ* (sex), *γ*’(sex), *γ*” (sex), *p*(sex,S1-S3,S4, S5,S6-S7), *c*(sex, S1-S3,S4,S5,S6-S7)}	20839.36	2.02	0.08	0.36	22	21680.67	20795.13
Detection Models	6	{ *φ* (.),*γ*’(.),*γ*” (.), *p*(sex,S1-S3,S4, S5,S6-S7), *c*(sex, S1-S3,S4,S5,S6-S7)}	20839.65	2.31	0.07	0.31	19	21687.02	20801.48
Transition Models	7	{ *φ* (.),*γ*’ (sex), *γ*” (.), *p*(sex,S1-S3,S4, S5,S6-S7), *c*(sex, S1-S3,S4,S5,S6-S7}	20840.75	3.41	0.04	0.18	20	21686.10	20800.56
Detection Models	8	{ *φ* (.),*γ*’ (.),*γ*” (.), *p*(sex,S1-S3,S4, S5-S7), *c*(sex, S1-S3,S4,S5-S7}	20842.69	5.35	0.02	0.07	15	21698.12	20812.59
	9	{ *φ* (.),*γ*’ (.),*γ*” (.), *p*=*c*(sex,S1-S3,S4, S5-S7)}	21079.05	241.71	0.00	0.00	9	21946.55	21061.01
	10	{ *φ* (.),*γ*’ (.),*γ*” (.), *p*(sex), *c*(sex)}	21273.11	435.77	0.00	0.00	7	22144.62	21259.08
	11	{ *φ* (.),*γ*’ (.),*γ*”*p*(.), *c*(.)}	21325.80	488.46	0.00	0.00	5	22201.32	21315.79
	12	{ *φ* (.),*γ*’ (.),*γ*” (.), *p*= *c*(.)}	21505.52	668.18	0.00	0.00	4	22383.05	21497.51

φ survival probabilities, *γ*’ = probability of temporarily leaving the study area given that animal was not present during primary period and unavailable for capture, *γ*” = probability of leaving the study area given that animal was present during primary period and unavailable for capture, S1 to S7 represents sampling session 2011 to 2017, *p*= Capture probability, *c* = Recapture probability,. The state and transition models are based on best detection models.

Table 3. 6: Model averaged survival and detection parameters estimates obtained from Robust design Analysis of CMR of 147 tigers between 2011 to 2017 in Kanha National Park.

Year	Capture Probability		Recapture Probability		γ'		γ''		Apparent survival (φ)	
	Male (± SE)	**Female(± SE)**	**Male(± SE)**	**Female(± SE)**	**Male (95% CI range)**	**Female (95% CI range)**	**Male (95% CI range)**	**Female (95% CI range)**	**Male (95% CI range)**	**Female (95% CI range)**
2011	0.12 ± 0.02	0.15 ± 0.01	0.17 ± 0.01	0.15 ± 0.01	0.46 (0.001-0.95)	0.08 (0.001 - 0.90)	0.06 (0.01 – 0.07)	0.03 (0.01 – 0.29)	0.78 (0.67 - 0.86)	0.84 (0.77 - 0.88)
2012										
2013										
2014	0.12 ± 0.02	0.17 ± 0.03	0.30 ± 0.01	0.29 ± 0.01						
2015	0.13 ± 0.02	0.12 ± 0.02	0.37 ± 0.02	0.25 ± 0.01						
2016	0.14 ± 0.02	0.16 ± 0.02	0.33 ± 0.01	0.29 ± 0.01						
2017										

φ survival probabilities, γ' = probability of temporarily leaving the study area given that animal was not present during primary period and unavailable for capture, γ'' = probability of leaving the study area given that animal was present during primary period and unavailable for capture.

3.4 Discussion:

This was the first study where both CMR and continuous monitoring (KF) models were used to estimate demographic parameters, which eventually provided an insight on tiger population ecology. Kanha tiger reserve is the largest source population of tigers in the central India and well connected to the neighbouring tiger reserves in a metapopulational framework. Long-term viability of Kanha tiger population will ensure recovery of tiger population in central india. Due to long-term research base and intensive monitoring of tigers by management in Kanha tiger reserve, crucial information on life histories parameters were recorded.

Reproductive parameters:

The mean litter size of Kanha tigresses were higher compared to any published literature (Smith & McDougal, 1991; Kerley et al., 2003; Singh et al., 2013). The Inter birth interval(IBI) and age of first reproduction of Kanha tigresses were lower compared to isolated Ranthambore tiger population (Sadhu et al. 2017); however, it was similar to Chitwan tiger population (Smith & McDougal, 1991) . Each breeding female can contribute 10 breeding tigers in her entire life span. Kanha tiger reserve is well connected to the adjacent tiger reserves like Pench, Navegaon-Nagzira, Achanakmar and Indravati tiger reserves in meta-population framework. There is good interchange of population occurred naturally by means of immigration and emigration, which eventually increase the chance of territorial conflict between tigers and results in infanticides. High reproductive potential in terms large litter size, shorter IBI and lower age of first reproduction are likely mechanism to compensate high cubs mortality due to infanticide.

Age-stage specific survival from Known fate:

The annual cubs survival (59.5%) was the lowest compared to other age classes of tigers in Kanha National Park. Twenty-four mortality events of cubs were recorded (16 infanticide, 01 poaching, 06 starvation due to mother death and 01 with unknown reason).Sixty-six percent deaths of cubs were mainly due to infanticide. Cub survival was similar to almost similar (61%) as reported by Schaller (1967) in Kanha national park. The annual survival probability increases after cubs stage and starts declining after prime adult stage (Table 3.4).The survivorship curve (Figure 3.2) explains that male tiger showed a typical Type II survivorship curve. Due to high overlap in home ranges, the territorial conflicts are more often in male tigers also due to their large home ranges they are more prone to poaching; hence, constant mortality regardless to age (Type II survivorship) is expected. The female tigers showed an intermediate curve between Type I and Type II survivorship. The home range size of females are smaller and exclusive (Sharma et al., 2010) hence territorial conflicts are less compared to males, hence, mortality is slightly age specific.

CMR based Robust Design Estimates:

In this study, tigers showed high capture probability due to intensive coverage of study area. Male tigers have large home ranges, so their interaction with camera traps are more often, hence, high capture probability compared to female tigers, which had smaller home ranges and restrictive in nature. The population estimates obtained through PRD was not different from estimates obtained by spatially explicit capture recapture (see chapter 2). The sampling area was constant since 2013 to 2017 hence parameters like recruitment, turnover and population change should be considered for this intervals while survival estimates is independent to varying sampling area. The tiger population within the national park had increased from 2013 to 2014 than declined for two years 2015-16 and again increased in 2017. This fluctuation in tiger population was likely due to synchronised reproduction by several females and recruitment of a large cohort of sub-adult in the increased year. The decline in 2015 and 2016 was likely due dispersal of sub-adult tigers from Kanha national park.

The survival estimates obtained from PRD are actually apparent survival, which are confounded with emigration and mortality. In carnivores males shows lower survival probability compared to females due to cost involves in dispersal and territorial conflicts (Bailey, 2005). In this study, the sex-specific point estimates of both apparent and true survivals are female biased, but possibly due to low sample size the 95% confidence interval of sex-specific survival estimates overlaps. The overall annual apparent survival estimates was 0.80 similar to (0.77) Nagarhole tiger reserve in south India ((Karanth et al., 2006) and (0.82) Huai Kha Khaeng Wildlife Sanctuary Thailand (Duangchantrasiri et al., 2016).

Recruitment and population turn over and dispersal:

The average recruitment rates were high for both the sexes (29% for males and 18% for females) with low precision because of fluctuating population. This corroborates the population turnover estimates of males and females. The difference between apparent survival and actual survival can be substantial if the size of the study area is small and permanent emigration or dispersal event occurred towards outside the sampling area (Zimmerman, Gutierrez, & LaHaye, 2007) . Here, in this case, the sampling area (940 km^2) was the largest for all published studies so far on tigers. Many of the dispersing individuals settled inside the study area after dispersing from their natal areas. Still, there was a difference between the survival estimates from Known fate and CMR based models. This indicates that there is substantial dispersal from Kanha tiger reserve to the adjacent forests. Taking into account of mortality rate from known fate and apparent survival probability from PRD model of this study, I estimated that about 9% of males and 8% of females annually dispersed outside to the study area.

The results of this study concede the importance of wildlife corridors between protected areas for long-term survival. Kanha is the largest source population in central India and well connected to the Pench, Achannakmar, Navegaon Nagzira tiger reserves. Kanha has also connectivity with Bandhavgarh and Indravati tiger reserves through a fragmented linear forest patch (Qureshi et al., 2014). The genetics evidence of emigration is the well-studied and genetic signature of Kanha tigers were found in Pench, Tadoba, Satpuda, Achankamar and Bandhavgarh tiger reserves (Yumnam et al., 2014)(S. Sharma et al., 2013). Yumnam et al. (2014) found 04 males and 01 female migrants from Kanha in Kanha Pench corridors. Photographic- evidence of dispersal from Kanha to Bandhavgarh were recorded based on the data from all India tiger estimation exercise of two cycles 2006 and 2010. On average, 07 tigers are annually dispersed (9% of the population size) from Kanha to repopulate the nearby tiger landscape. The long-term persistence of Kanha tiger population is essential for landscape-level sustenance.

CHAPTER 4. DEMOGRAPHY OF LEOPARD

4.1 Introduction:

Data on the population dynamics are vital to evaluate the conservation measures, but this is impeded by the lack of studies. Leopard is one of the most widespread carnivores (Nowell & Jackson, 1996)(Hunter & Barrett, 2013.) but information on population dynamics such as survival and reproductive parameters are remarkable scares and currently limited to the African subspecies (*Panthera pardus pardus*)(see (Balme, Slotow, & Hunter, 2009)(Owen, Niemann, & Slotow, 2010), (Swanepoel et al., 2015). Indian Leopard (*Panthera pardus fusca*) has lost 70-72% of the its historic range, due to habitat fragmentation, poaching and retaliatory killing(Jacobson et al., 2016). (Raza et al., 2012) did a comprehensive study on seizures of leopard body parts and estimated that on average, four leopards were poached every week in India based on the seizures between 2001 to 2010. Indian leopards are extensively distributed throughout the forested habitat except in mangroves forests and deserts. They are well adapted and pliable to survive near high human density outside protected areas (PAs). A sizable population of leopards are outside the PAs (Jhala, Qureshi, & Gopal, 2015) currently under severe threat due to conflict with human interests (Jacobson et al., 2016). Leopards get considerable protection within most of the PAs along with their bigger congeneric tigers and lions. Tiger and lions are known to regulate leopard population by direct competitive exclusion (Balme, Slotow, & Hunter, 2009; McDougal , 1988). Competitive interaction with tiger may affect densities and survival of leopards, and leopard populations were found to decline in areas of growing tiger populations (Harihar, Pandav, & Goyal, 2011; Edgaonkar, 2008). The

Indian leopard population are likely declining (Jacobsen et al. 2016), and information on their survival and recruitment are completely absent, these parameters are important to device any recovery strategy. Most of the studies on Indian leopard are limited to snapshot population estimates(Harihar, Pandav, & Goyal, 2011),(Kalle et al., 2011) Kalle et al. 2011) or on their interaction with humans (Sangay & Vernes, 2008)(Athreya et al., 2013)(Athreya et al., 2015)

The development of capture-mark-recapture (CMR) based field and analytical methods provide an excellent tool to estimate abundance of elusive carnivores, which can be individually identifiable through their unique body marking(K U Karanth, 1995). Leopards can be uniquely identified through their rosette pattern (Sunquist & Sunquist, 2002). However, leopards have low detection rate in camera traps, especially in the areas where they share their resources to congeneric large carnivores. The density and other population parameters estimate based on low detection rate are imprecise and of limited value to the ecologist and wildlife managers (Braczkowski et al., 2016) Due to low detection in camera traps the capture-recapture information are mostly zero-inflated. The zero-inflated data have analytical limitations such as parameter un-identifiability and redundancy (Gimenez, Grégoire, & Lenormand, 2009). The survival estimates from zero-inflated data are very imprecise, and it is challenging to find any sex-specific differences in parameters due to overlapping confidence intervals (Gimenez, Choquet, & Lebreton, 2003) The development of spatial capture-recapture models, especially in the Bayesian framework, which examines posterior means based on prior information and Markov chain Monte Carlo simulations, are robust to parameter redundancy and un-identifiability, and results are more precise compared to non-spatial open population models (Gimenez, Choquet, & Lebreton, 2003; Whittington & Sawaya, 2015).

In this chapter, I present my study on the demography of leopard in the PA of Kanha tiger reserve with CMR based non-spatial and spatial open population models to estimate survival and recruitment parameters.

4.2. Methods:

Study design (Camera trapping):

I used multi-year camera trap based capture-mark-recapture (CMR) framework to estimate apparent survival probabilities and per capita recruitment. Initially, due to limited logistic, I sampled the survey area in two blocks with a total area of 460 km^2.

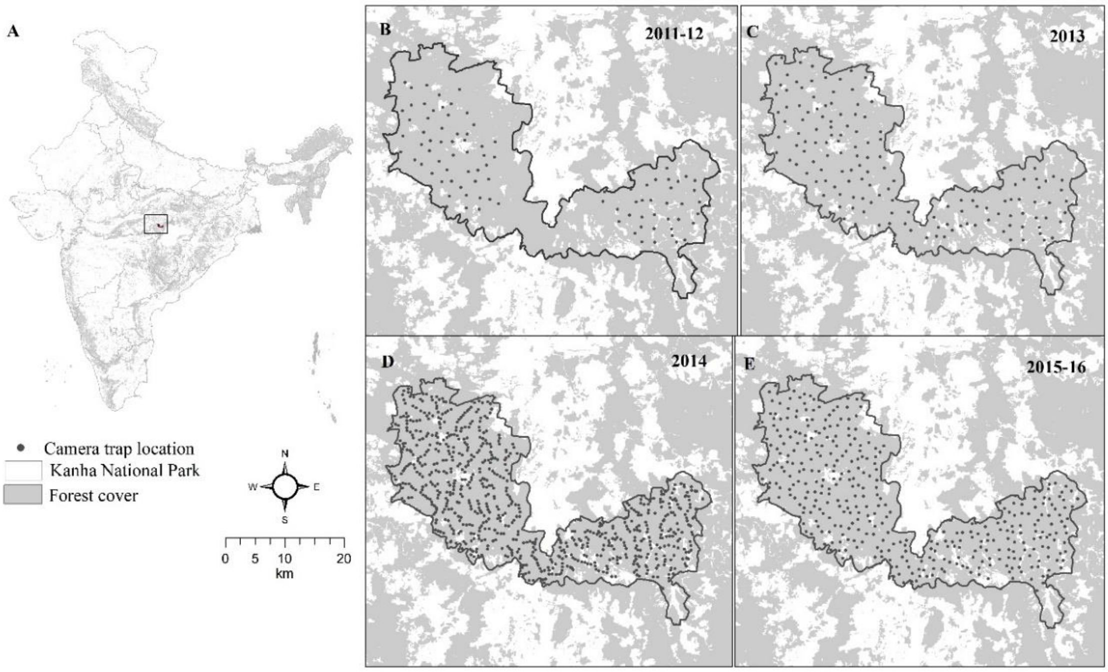

Figure 4. 1: Camera trap locations in Kanha National Park (A) Kanha National park within India (B-E) Camera locations in Kanha National park.

Later with the increase in resources, I gradually increased the sampling area in subsequent years (Table 4.1). Since 2013 onwards, the entire National Park of 916

km^2 was sampled with camera traps. With the extra resources, the camera densities were subsequently increased from 2014 to gain better precision on the estimates (Table 4.1.). Camera trap locations were selected to maximise photo captures of leopards after extensive sign surveys on forest roads, trails and streambeds (Figure 4.1).

Table 4. 1: Sampling Effort for Leopard demography study in Kanha National Park.

Sampling Year	**Camera Locations**	**Trap night Effort**	**Sampling area (km^2)**	**Average Trap distance (km ± SE)**	**Unique Individual (M_t+1)**		
					Males	**Females**	**Unidentified sex**
2011	96	4210	460	1.74 ± 0.039	17	17	1
2012	127	4837	660	1.77 ± 0.005	21	20	1
2013	155	7191	916	1.73 ± 0.032	22	28	7
2014	758	18782	916	0.52 ± 0.005	35	48	1
2015	384	11584	916	1.05 ± 0.012	41	40	4
2016	384	17391	916	1.05 ± 0.012	38	62	5

Data preparation and Analysis

Leopard identification:

To minimise the human error, identification of unique leopard was done through programme HotSpotter (Crall, J. et al., 2013). Database of unique leopards from annual camera trapping exercise since 2011 to 2016 were made. The gender and age of each leopard were ascertain based on genitals and secondary sexual characters, cubs of less than a year of age were excluded because of low detection probability and possible high mortality (Karanth & Nichols, 1998)

Non-Spatial Open population model (survival estimates):

The classical non-spatial CMR Open population models are based on the capture-recapture events of the individual animal during the multi-session sampling. The non-spatial CMR Open population models were developed, where only survival can be estimated Cormack-Jolly- Seber (CJS), and a fully open model Jolly-Seber (JS) for estimating both recruitment and survival(Cormack , 1964; Jolly, 1965,) Seber, 1965). Later robust design open population models(PRD) were developed by combining open and closed model to get abundance, survival and temporary emigration parameters ((Pollock, 1982; Kendall & Bjorkland, 2001). The PRD models have the advantage over CJS and JS model by few reasons (i) abundance can be estimated without the assumption of equal catchability (ii) recruitment can be separated from birth and immigration if multi-stage information of an individual is available (Kendall, Pollock, & Brownie, 1995)(Kendall and Pollock 2001). However, PRD models require good recaptures, sufficient data during the secondary period of the sampling to get fair convergence of parameters. Which was lacking in the case of leopards due to their highly secretive nature compared to tigers. I used Cormack Joly Seber (CJS) open model (Cormack 1964; Jolly 1965; Seber 1965) to estimate the apparent survival estimate of leopard. CJS model only estimates apparent survival, and it does not model the first capture of the individual animal, it's model the recapture probability conditioned on the first capture. The apparent survival estimates from the CJS model are robust and used maximum likelihood estimator (Lebreton et al., 1992) The CJS model provides unbiased estimates of survival when temporary emigration is random; in this case, there was no any reason to believe that the temporary emigration is non-random. I modelled constant effect, time/session and sex-specific variation on parameters and then selected best models based on the lowest Akaike information criteria score corrected for small sample size (AICc). Data were analysed through package RMark ver2.2.5 (Laake, 2013) in the R programming environment. Model averaging (for less than 10 dAICc) was done to account for uncertainty in model selection(Burnham & Anderson, 2002).

Spatial Open population model:

The recent development of spatially explicit capture-recapture models (SECR or SCR: (Borchers & Efford, 2008a)(Royle et al., 2009) allows the use of the spatial locations of sample data to estimate densities. However, most of the SCR based analysis is limited to closed population models for snapshot estimates of densities. Very recently SCR based open population models which considers estimation of important demographic parameters such as survival probabilities (φ), per capita recruitment (Υ)and population trends (Chandler & Clark, 2014; Ergon & Gardner, 2014) have been developed.

Spatial explicit capture-recapture (SECR/SCR) models have an advantage over classical non -spatial open models since they account for individual heterogeneity in capture by estimating activity centres and a spatial scale parameters that describe the detection as a decreasing probabilities with distance to the home range activity centre (Borchers & Efford, 2008b; Royle et al., 2009) The open SCR models also incorporate immigration and emigration processes by allowing individuals to shift their activity centre between primary periods moving in or out from the sampling area i,e. emigration. This is modelled by using a dispersal kernel that has a single spatial scale parameter determining the extent of movement within the state space (Ergon & Gardner, 2014) However, the delineation of state space where dispersal can happen is crucial for this type of models, and the estimates could be biased if biologically meaningful state space is not provided (Gardner et al., 2018) In this case, my sampling area was the entire National park of 940 km^2, and I provided a rectangular state space of 4975 km^2 by buffering 14 km to the outermost sides of sampling area coordinates. I believe this vast area of about 5000 km^2 would likely suffice to model the leopard dispersal based open population SCR based models. The tigers are limited to forests with minimal human presence but leopard habitat extends across scrub, pasture, agriculture and fragmented forests close to human habitation. Hence, use these landscape categories in this rectangular state space was realistic for the leopard dispersal model.

I used a hierarchical, gender-specific, open population SCR model, accounting for activity centre shift between primary period implemented in R package OpenPopSCR (Augustine, 2018; Satter et al., 2019) to estimate annual survival probabilities (φ^m, φ^f), per capita recruitment rates (Υ^m, Υ^f), and population growth rates of the leopard in Kanha national park over the 6-year period between 2011-2016.

Data structure: The data consisted of trap and capture matrices – The trap matrix consists of trap locations in xy format and its operational days (1= operational, 0 = not operational on the day) for each primary period. The capture matrix consists of the primary period as session, animal id, the occasion at which animal was captured during the primary period, the trap location where the animal has been captured and the gender of the individual animal (1= male 2 = female, NA = unknown gender). The data were collapsed into a 3-dimensional array ($n \times J_{max} \times L$) for processing under the model. Here, n = total number of individuals captured overall year, J_{max} = maximum number of traps in any year, L= the number of sessions

Process model: I used the density-independent population growth model with sex-specific growth and detection function (Skalski, Ryding, & Millspaugh, 2005). The sex-specific parameters were survival probabilities (φ^m, φ^f), per capita recruitment rates (Υ^m, Υ^f) and the abundance ($\widehat{N}^m$, $\widehat{N}^{f)}$.

Observation model: : In each year *l*, leopards were observed at camera locations $\boldsymbol{X}_l$ over K_l occasions, recorded as binary detection events and then summed over occasions. Therefore, it was assumed that observation of individuals by trap by year number were distributed as $y^m{}_{ijl} \sim Binomial(p^m{}_{ijl}, K_l)$ and

$y^{f}_{ijl} \sim Binomial(p^{f}_{ijl}, K_l)$ for males and females, respectively, where p^{m}_{ijl} and p^{f}_{ijl} are the sex-specific individual by trap by year capture probabilities, I fitted a hazard half normal detection function conditional on the yearly activity centres (Royle et al., 2014). The detection function parameters were sex-specific baseline encounters (~detection probability at home range centre) (λ_0^{m}, λ_0^{f}) and spatial scale parameters (σ^{m}, σ^{f}). The sex-specific parameters determine the probability of unknown sex individual of a specific sex. If it has a large spatial recapture, more likely to be male.

Markov Chain Monte Carlo (MCMC) inference: I estimated model parameters, through MCMC algorithms using data augmentation (Chandler & Clark, 2014; Royle et al., 2014) via the OpenPopSCR R package (Augustine, 2018).The augmented population M was chosen to be much larger than the expected number of individuals alive across all years here I choose M=1000 since it was 10 times larger than the numbers of photo-captured unique leopards. I ran two models with sex-specific parameters.

1. Fixed activity centre model: I first model by assuming no change in activity centre during the sampling of six-year primary periods. This model is equivalent to apparent survival estimates from non-spatial open population models. I sampled from posteriors of 1.5 Lakh iterations, discarding 10000 iterations as burn-in. The remaining samples were pooled for posterior inference. Posterior modes and 95% highest posterior density (HPD) intervals were estimated.
2. Markov model (Change in activity centre): The second model was based on assumption and ecological reality that leopards disperse and

emigrate from their natal area after attaining the age of 2-4 years(Bailey, 2005). Hence, the activity centres may change during primary periods. In this model, the activity centres were allowed to shifts by Markovian movement. It assumed that in the first primary period the activity centres are distributed uniformly across the state space and in subsequent primary period (next years) are drawn from bivariate centred normal distribution. The Markov model estimates another spatial scale parameter dispersal sigma (σt) based on shift in activity centre. Females are mostly philopatric, and males disperse to a larger distance from their natal area. Hence, I modelled sex-specific dispersal along with the survival and per capita recruitment. I sampled from the joint posterior using 20 chains of 10000 iterations each, discarding 2500 iterations as burn-in for each chain. The remaining samples were pooled for posterior inference. Posterior modes and 95% highest posterior density (HPD) intervals were estimated.

Model convergence were checked through $\widehat{R}$ (Spiegelhalter et al., 2013). $\widehat{R}$ is Gelman-Rubin convergence statistic, modified by Brooks & Gelman, (1998). $\widehat{R}$ value less than 1.1 are considered satisfactory.

Decision rule to test significant differences between male and female demographic parameters: In the frequentist approach, the significant difference between two groups is mainly checked by t-test or measure of overlap in 95% confidence interval. However, this method has a limitation, as in the real world survival and recruitment are continuous measures, and there is no chance that it will be the same for males and females. In addition, the confidence intervals (CI) do not have distribution information; hence, the uncertainty in the parameter estimates are not drawn directly from distribution. Although, many statisticians developed methods by superimposing sampling distributions or relative likelihood curves on the CI (see (Cumming & Fidler, 2009; Cumming, 2014), but neither of these approaches provide the probability of the parameter values (Kruschke & Liddell, 2018). In Bayesian statistics, the uncertainty of the estimate is exceptionally determined by the spread of the posterior distribution and the confidence interval is replaced by posterior highest density interval (HDI) (Kruschke, 2014). The Bayesian statistics doesn't work on the null hypothesis, however, for understanding whether there are any sex-specific differences in the demographic parameters. I developed a null hypothesis that the demographic parameters are not different between males and females. To test the difference between sex-specific parameters, I measured the amount of posterior distributions of the parameters that lies inside the region of practical equivalence (ROPE) along with a posterior highest density interval (HDI) (Kruschke & Liddell, 2018).

If the required HDI falls entirely outside the ROPE than we could conclude that, there is evidence of sex-specific differences in the demographic parameters I used Wiqid and BEST package in R (Kruschke & Meredith, 2018; Meredith, 2019) to calculate the differences between the posteriors of sex-specific parameters and plotted to see how much HDI lies in and outside of the ROPE. The posteriors of ecological plausible Markovian model was further processed to derive the estimates of realized population growth rate (λ) and sex ratio. The estimated populationfor the entire state space was based on the information from the sampling space.

Since Bayesian approaches uses λ_0 to depict base line encounter rate at home range/Activity centre, I clarify that λ without subscript of 0 is population growth .

4.3 Results:

A total sampling effort of 63995 camera trap nights provided 3978 usable photographic captures of 217 unique leopards (78 males, 120 females and 19 of unknown gender) during the six years of the study (2011-2016). Individual leopards with unknown genders were not recaptured in any subsequent primary periods; hence, they were not used in estimating CJS based survival estimates. However, spatial capture-recapture open models allows the use of unsexed individuals in their sex-specific models by assigning them to sexes based on the similarity of detection parameters.

Non-spatial open CMR (CJS) survival estimates:

Although the best model was explained by the each year (primary period) and sex varying recapture probability but survival rates did not change with sex or time ($p \sim t + sex\ \varphi \sim 1$) (Table 4.2). However, there was high model uncertainty as several models had nearly identical AICc values, and therefore, model-averaged estimates were reported (Table 4.3). The point estimates for female survival (0.70 ± 0.04) was lower than male survival (0.72 ± 0.05) leopards. Although the 95% CI level range overlaps, hence there is no significant difference between male and female survival estimates through the CJS model.

Table 4. 2: Model selection table for CJS Analysis of Leopard data in Kanha NP.

Models	npar	logLik	AICc	AICc	Deviance
φ (~1)*p*(~sex + time)	7	511.69	0.00	0.43	85.85
φ (~sex)*p*(~sex + time)	8	513.37	1.68	0.19	85.41
φ (~1)*p*(~sex * time)	11	513.70	2.01	0.16	79.30
φ (~sex)*p*(~sex * time)	12	513.80	2.11	0.15	77.23
φ (~time)*p*(~sex + time)	11	517.39	5.69	0.03	82.99
φ (~1)*p*(~sex)	3	518.27	6.58	0.02	100.74
φ (~sex + time)*p*(~sex + time)	12	519.29	7.60	0.01	82.72
φ (~sex)*p*(~sex)	4	520.27	8.57	0.01	100.68
φ (~time)*p*(~sex * time)	15	521.09	9.40	0.00	77.89
φ (~sex + time)*p*(~sex * time)	16	521.19	9.50	0.00	75.75
φ (~sex * time)*p*(~sex)	12	522.23	10.54	0.00	85.66
φ (~time)*p*(~sex)	7	523.66	11.97	0.00	97.82
φ (~sex * time)*p*(~sex + time)	16	524.12	12.43	0.00	78.68
φ (~sex + time)*p*(~sex)	8	525.32	13.63	0.00	97.36
φ (~1)*p*(~time)	6	525.74	14.05	0.00	101.99
φ (~1)*p*(~1)	2	526.27	14.57	0.00	110.78
φ (~sex)*p*(~1)	3	526.41	14.72	0.00	108.88
φ (~sex)*p*(~time)	7	526.60	14.91	0.00	100.76
φ (~sex + time)*p*(~1)	7	527.56	15.87	0.00	101.72
φ (~time)*p*(~1)	6	529.07	17.38	0.00	105.33
φ (~sex * time)*p*(~sex * time)	20	529.76	18.07	0.00	75.20
φ (~sex + time)*p*(~time)	11	529.88	18.18	0.00	95.48

npar = No. of Parameters, logLik = Log likelihood

Table 4. 3: Model average estimates of recapture probability (p), and annual survival (φ) from open-model Cormack–Jolly–Seber analysis based on photographic capture data from Kanha National Park from 2011 to 2016.

Year	$p_{Females}$ ± SE	p_{Males} ± SE	$\varphi_{Females}$ ± SE (range 95% CI)	φ_{Males} ± SE (range 95% CI)
2011	**NA**	NA	0.70 ± 0 .04 (0.61 – 0.77)	0.72 ± 0.05 (0.62 – 0.80)
2012	0.60 ± 0.14	0.87 ± 0.09		
2013	0.52 ± 0.13	0.86 ± 0.07		
2014	0.75 ± 0.11	0.96 ± 0.03		
2015	0.55 ± 0.09	0.90 ± 0.05		
2016	0.98 ± 1.34*	0.96 ± 0.04		

***** Parameter redundancy

Open population spatial capture recapture model estimates:

Both the Bayesian models converged at the given iterations the $\hat{R}$ was less than 1.1 for posterior plots (see Figure 4.2 & 4.3).. The movement parameter σ was sex specific; females having smaller movement compared to males. Similarly, the dispersal σ (estimated from Markov models) was also higher in males compared to females. It was evident from the ROPE plot (Figure 4.4) that the demographic estimates differed between sexes for both models. Female had less survival with high recruitment rate compared to males, which had higher survival probability and low recruitment rate (Table 4.4). The survival rate was improved after accounting for the shift in activity centres during subsequent primary period. The sex ratio was consistently female biased across the six year 2011 to 2016 (Table.4.5). Annual change in the population was mainly driven by female population growth (Table 4.5).

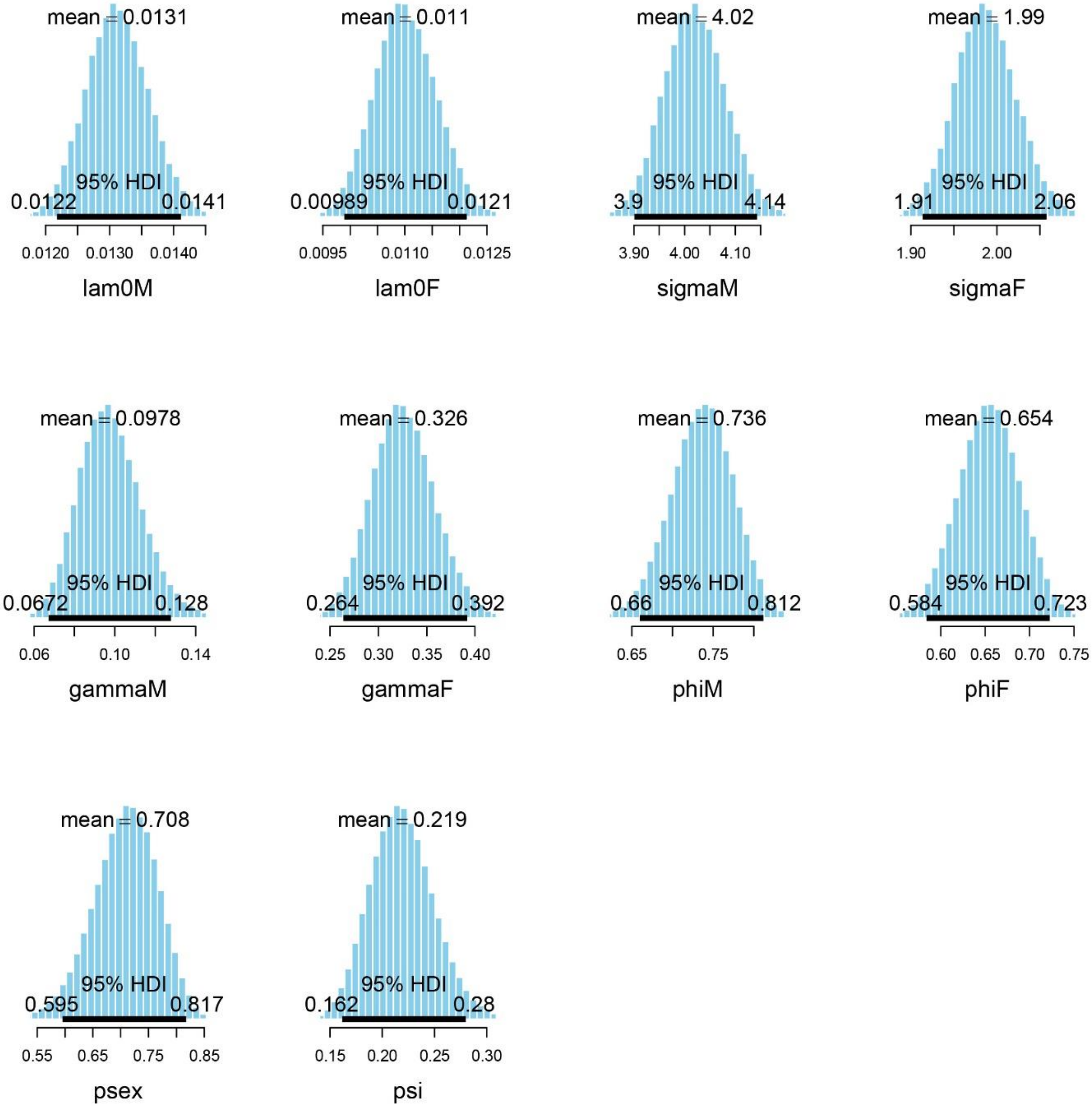

Figure 4. 2: Posterior plots of Fixed Activity Centre model parameters.

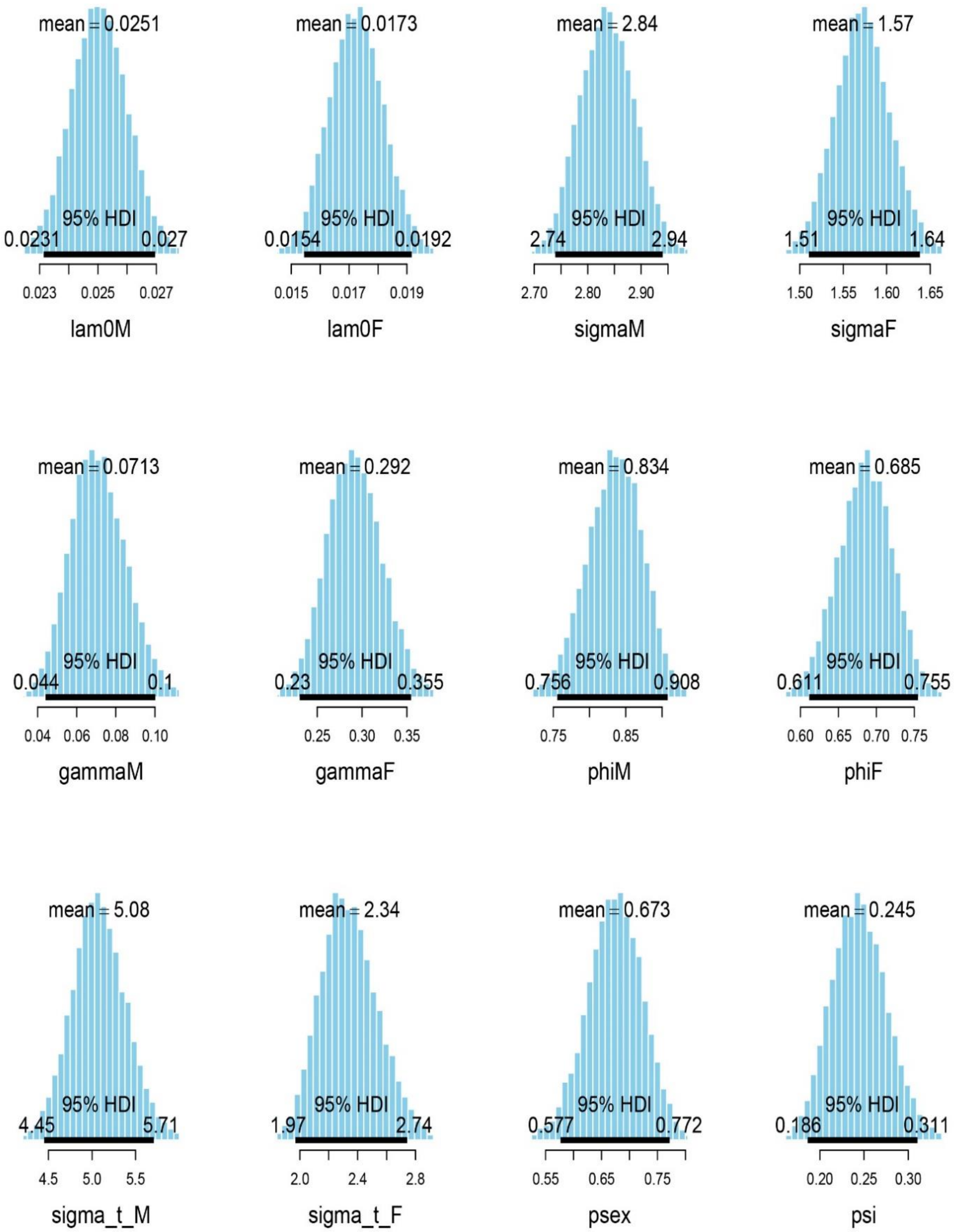

Figure 4. 3: Posterior plots of Markov change in Activity Centre parameters.

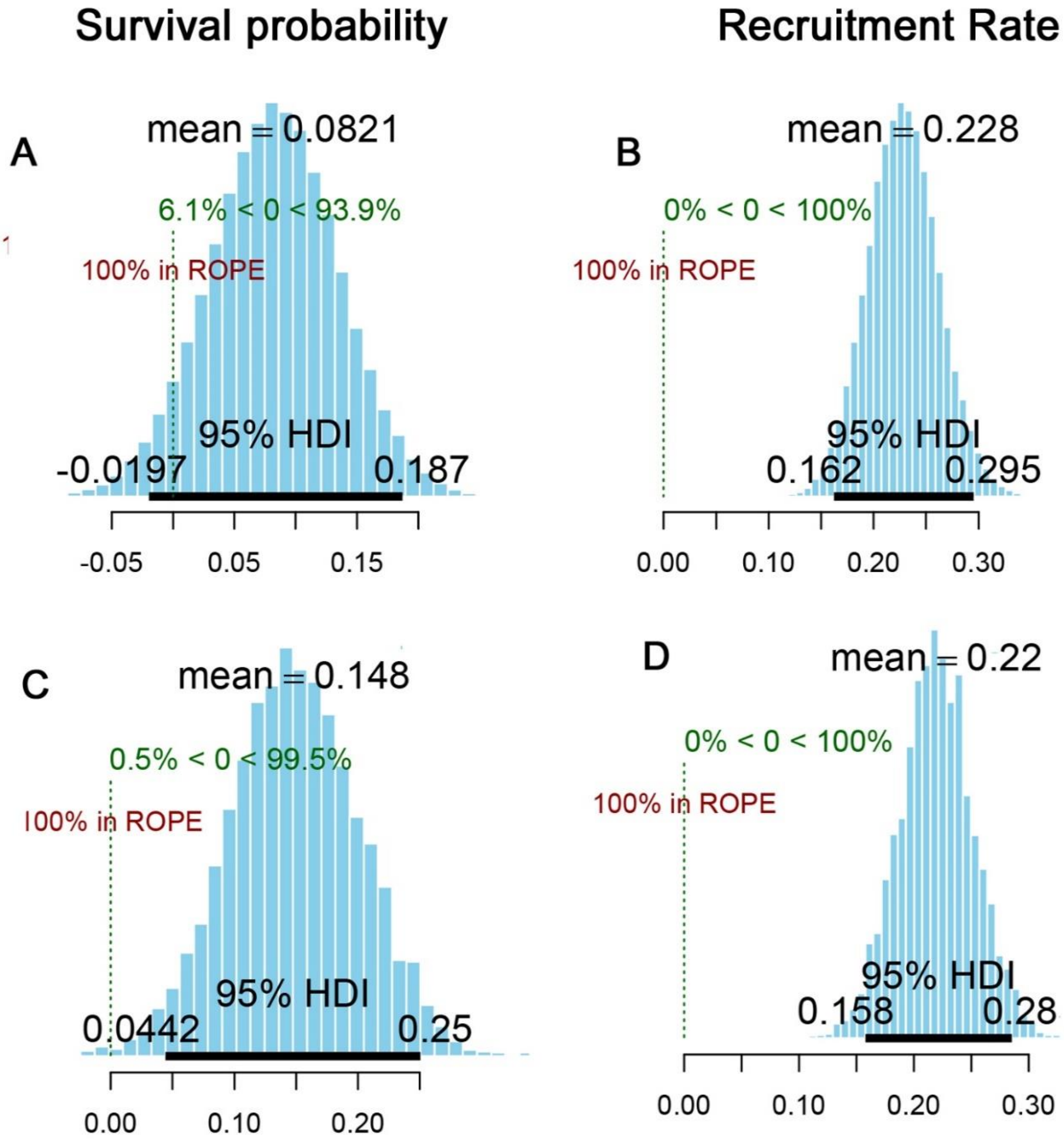

Figure 4. 4: ROPE plot: sex-specific difference in the posteriors of the survival and recruitment parameters falling inside the region of practical equivalence (here the width of ROPE -1 to 1).

Table 4. 4: Parameter estimates from openSCR models.

Parameters	**Fixed AC Model estimates (95% HDI range)**	**Markov AC Model estimates (95% HDI range)**
Male survival rate φ^{m}	0.74 (0.66 – 0.81)	0.83 (0.76 – 0.91)
Female survival rate φ^{f}	0.67 (0.59 – 0.73)	0.69 (0.61 – 0.75)
Male base line encounter λ_0^{m}	0.01 (0.012 – 0.014)	0.03 (0.02 – 0.027)
Female base line encounter λ_0^{f}	0.01 (0.001- 0.012)	0.02 (0.015 - 0.019)
Male Sigma σ^{m}	4.02 (3.91 – 4.17)	2.84 (2.73 – 2.93)
Female Sigma σ^{f}	1.99 (1.92 – 2.06)	1.58 (1.50 – 1.63)
Male per capita recruitment rate Υ^{m}	0.11(0.07 – 0.14)	0.07 (0.04 – 0.10)
Female per capita recruitment rate Υ^{f}	0.32 (0.25 – 0.36)	0.29 (0.22 – 0.35)
Male Dispersal Sigma $\sigma^{m}t$	NA	5.05 (4.48 – 5.73)
Female Dispersal Sigma $\sigma^{f}t$	NA	2.36 (2.02 – 2.73)

Table 4. 5: Estimates of Population (in the state space Kanha NP + Buffer of 15km), realized growth rate and sex ratio of Leopards.

Year	**$\hat{N}$** (95% HDI range)	**$\hat{N}_{Male}$** (95% HDI range)	**$\hat{N}_{Female}$** (95% HDI range)	**λ** (95% HDI range)	**λ_{Male}** (95% HDI range)	**λ_{Female}** (95% HDI range)	**Sex ratio (M:F)** (95% HDI range)
2011	243 (184-294)	76 (56-100)	157 (117-208)	NA	NA	NA	0.67 (0.59 - 0.75)
2012	270 (212-310)	80 (62-100)	186 (140-222)	1.06 (0.99 - 1.19)	1.0 (0.90 - 1.20)	1.13 (0.98 - 1.27)	0.69 (0.63- 0.75)
2013	283 (243-331)	83 (67-103)	200 (164-240)	1.08 (1.01 - 1.20)	1.0 (0.92 - 1.20)	1.14 (1.0 - 1.25)	0.69 (0.65- 0.75)
2014	314 (272-354)	92 (75-111)	212 (180-255)	1.08 (0.99 - 1.17)	1.0 (0.95 - 1.23)	1.08 (0.97 - 1.19)	0.70 (0.64 -0.75)
2015	347 (300-389)	100 (84-123)	245 (197-279)	1.09 (1.01 - 1.18)	1.10 (0.98 - 1.23)	1.09 (0.99-1.20)	0.70 (0.64 - 0.75)
2016	389 (322-434)	100 (85-132)	261 (220-321)	1.09 (1.02 - 1.18)	0.99 (0.95 - 1.18)	1.12 (1.02-1.22)	0.71 (0.65 - 0.77)

4.4 Discussion:

In this study, I estimated sex-specific survival, recruitment and population growth of leopards within the Kanha national park. Two methods of open population models the traditional non-spatial capture-recapture and the spatial capture-recapture were used to estimate survival probabilities. Non-spatial models cannot differentiate between mortality and emigration, but the Bayesian spatial open population models allow to model the movement and separate emigration from mortality, it provides more realistic estimates of demographic parameters with fewer restrictive assumptions (Ergon & Gardner, 2013; Satter et al., 2019). In addition, open SCR models have an advantage over non-spatial open CMR population model in accounting for varying extent of sampling area for estimation other demographic parameters such as recruitment, and population trend. This study was the first to estimate sex-specific survival and recruitment estimates of leopards through long term CMR based sampling Sex-specific population growth rate were also reported.

Survival and dispersal:

In carnivores, low survival is mostly biased towards male since they have to bear the cost of dispersal far from their natal territory and competition for females. Nevertheless, contrary to this belief, I found lower survival probability for the female leopards using both approach of open population models. However, this sex-specific difference was only significant in the Bayesian open SCR models. The non-spatial open CMR model results in similar apparent survival probability for male (0.72 range 0.62- 0.80) and female (0.70 range 0.61- 0.77). Even though there is no robust estimates are available for comparison, this estimate was similar (0.71) to (Mondal et al., 2012) at Sariska tiger reserve. The Bayesian open SCR fixed AC model estimates actually provide the apparent survival estimates since it does not account for shift in animal activity centre during the subsequent years. The open SCR fixed AC model survival estimate was significantly different between male and females but similar to non-spatial CMR based survival estimates. When the open SCR with shift in activity centre modelled, (Markov AC) survival estimates were improved and were likely to be close to true survival since these models account for dispersal. The movement parameter σ for the both sexes decreased as a new movement parameter of shift in activity centre during subsequent years dispersal sigma (σ_t) was accounted in the model. The dispersal sigma (σ_t) was significantly higher for males (5km) and its corroborate that males disperse further from their natal territory however female's dispersal sigma was less (2km) since females are more philopatric. Dispersal rate was obtained by subtracting Markov (true survival) and Fixed (apparent survival) activity centres models based estimates. It was found that 9% of the male disperse outside the PA while only 2% of the female left their natal territory. High mortality (33%) in female leopards compared to male leopards (13%) from Markov AC model was reported. For comparison, the sex-specific survival estimate of leopards is only available from southern Africa by Swanepoel et al., (2015) and similar higher male-biased survival was reported.

Recruitment, sex ratio and population growth:

Overall leopard population showed positive growth ($\lambda = 1.18$ range 1.004 – 1.21) mostly determined an increase in females. The sex ratio was overall female biased throughout the sampling years. Average recruitment rate in the population was high for female and low for male; this indicates such scenario i,e. low survival but higher proportion in the population and high recruitment is possible only if sex ratio at birth skewed towards females. The high mortality of female was compensated by higher recruitment rate to give a female biased sex ratios. This could be likely a function of high tiger density in the PA, and female leopards are vulnerable to intraspecific predation by tiger due to their small home range size and higher spatial philopatry. Leopards are most persecuted carnivore due to human-leopard conflict amongst all carnivores in Asia (Holland et al. 2018). Due to rising conflicts with humans and increased poaching, the leopard population is in threat (Stein et al., 2016). To device, any conservation strategy for the leopards, information on their population dynamics is important. The central Indian forests support the largest leopard population in India sympatric with the tiger in the majority of the PAs (Jhala, Qureshi, & Gopal, 2015). This study was the first to used a novel non-invasive methods to better understand to demography of leopards.

CHAPTER 5. COEXISTENCE AND RESOURCE PARTITIONING BETWEEN TIGER AND LEOPARD

5.1 Introduction:

Sympatric species of similar guilds can potentially compete for resources such as food and space(Putman, 1996). Such competition often can be detrimental to either or both species (Lovari et al., 2014). Competition for resources are more severe when two sympatric carnivores exploit similar and limited resources. Resource partitioning at the scale of diet, space use and activity allow such sympatric carnivores persist and avoid lethal encounter with the more dominant species (Palomares & Caro, 1999). Tigers co-occur with the leopards in their entire range except in mangrove forest of Sundarbans in India. Both top predators have similar diets. Large investment in the form of Protected Areas, human resettlement, law enforcement-patrols and habitat management are made to conserve tigers and reap their benevolent umbrella role to secure India's biodiversity (Project tiger 2019). Tigers being apex predators out-compete and often kill other predators like leopards, dhole, and sloth bear(McDougal, 1988). In areas of high tiger densities, leopard were likely out-competed (Harihar, Pandav, & Goyal, 2011). High tiger density areas like Corbett and Kaziranga National Parks though having abundant prey, have very few leopards (Firoz Ahmed et al., 2010; Jhala, Qureshi, & Gopal, 2015) Habitats without escape refugia from tigers were devoid of leopards e.g. the mangrove swamp forests of Sundarbans. Understanding population response of leopards at local scales to tigers would provide insights on thresholds of the benevolent effect of tigers on sympatric large carnivores and at what densities tigers become detrimental to other threatened carnivores. Tiger and leopard co-exist together by resource partitioning, such that leopards are displaced towards periphery of the PAs and sub-optimal habitat (Seidensticker, 1976) by tigers, they use different time scale (activity) to track their prey species(Ramesh et al., 2012).

In this chapter, I presented, how tiger and leopard partition their resources within Kanha Tiger Reserve, Madhya Pradesh India, a major stronghold for both species in Central India.

5.2 Method:

Spatial Partitioning:

Camera trap based mark-recapture framework (Karanth, 1995)was used to estimate spatially explicit densities of tiger and leopard (Borchers & Efford, 2008) Since SECR models are spatially explicit in nature, they produce fine scale density maps (Royle et al., 2014). Since 2013 to 2016 the entire core area of Kanha tiger reserve i.e. Kanha National Park was sampled, to understand the demographic response of tiger and leopard to each other. Method for camera trapping is detailed in the section on sampling design described in chapter 2 of the thesis. Spatial variation maps of tiger and leopard densities within the sampled area with a buffer of 3 km width (equal to one σ of tiger and leopard) were generated. To understand how leopard population responds to the density and growth of tigers at the scale of a home range of breeding tigresses (10 km^2) in Kanha National Park (Shrama et al. 2009), densities and growth rates (r) of tigers and leopards in each grid of 10 km^2 were extracted. For each grid, I estimated the growth rate (r) for both carnivores by regressing Ln (density) against years. Contour plots for leopard growth rates against tiger density and against tiger growth rates were drawn to evaluate the demographic response of leopards to tiger demography in NCSS 11. I hypothesize that tiger densities decline with increasing distance from PA boundary(core zone or Kanha Natioanl Park), however leopards being more adaptive to human modified landscapes would potentially would not respond to distance from PA. For this analysis, I used spatial densities of 2014, since during this session entire tiger reserve which includes the protected area (PA)) and the multiple use buffer zone were sampled together (Figure 5.1). I estimated densities and sex ratios for both the species for both core and buffer zones for 2014 data sets. Akaike Information Criteria corrected for sample size (AICc) was used select the best model that explained the observed data. To account for model uncertainty (Burnham & Anderson, 2002), I used AICc weighted model averaging for parameter estimates.

At the home range scale of breeding tigress (10 km^2) grids in Kanha, I extracted spatial densities of both predators and Euclidian distance to core zone in ArcGIS 10.2. First, I did exploratory analysis by plotting predator densities against distance to core zone (Figure 5.4). By visualizing the scatter plot, I found some evidence of multiple slopes. Quantile regression is useful in estimating multiple rate of change from minimum to maximum response(Koenker & Bassett, 1978; Cade & Noon, 2003). I used quantile regression and reported coefficients at 0.5, 0.75 and 0.90 quantiles. These quantiles was useful in interpreting the response of upper threshold of maximum possible densities with increasing distance to PA.

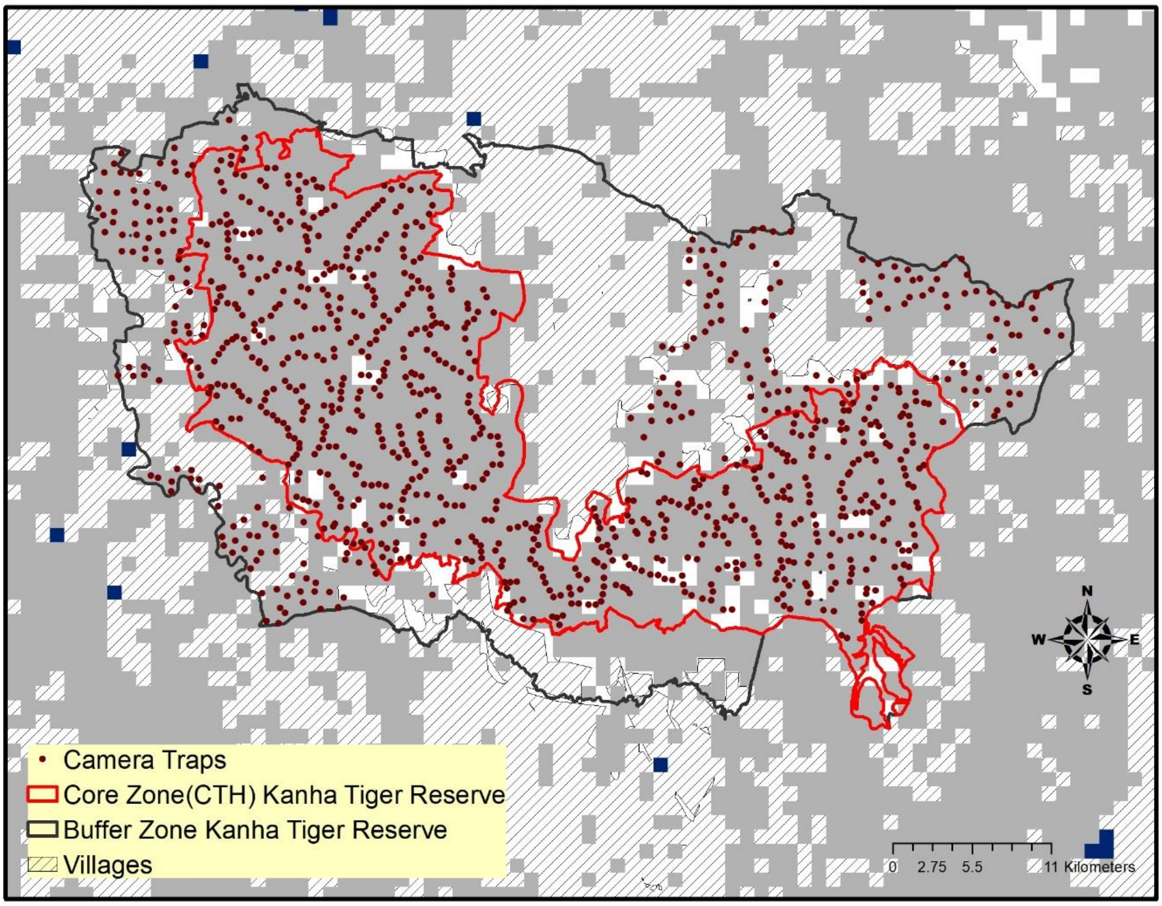

Figure 5. 1: Camera trap design at Kanha Tiger reserve (core and Buffer) in 2014.

Temporal Partitioning:

To assess the temporal activity pattern of tiger and leopards in Kanha tiger reserve, I used time of photo-capture obtained from the camera trap pictures. Fifteen minutes interval between two consecutive times of photo-capture were kept to consider independent capture event. Activity pattern of species overlap between the activity of tigers and leopards were computed in R package ‘overlap’ vers.0.2.4 (Meredith & Ridout, 2014).

Diet composition and overlap:

I collected tiger and leopard scats (tiger n = 325 and leopard n = 228) to analysed the prey remains in scats. Scats were collected during sign survey on forest roads and animal trails during May to June 2013. Scats were sun dried for 72 hours, before being preserved in polythene bag filled with silica gel for long-term storage. Species identity as tiger's or leopard's scats were later verified through genetic analysis (Yumnam et al., 2014). A total of 180 scats of tiger and 133 scats of leopards were confirmed. I estimated the proportional contribution of different prey items to a single scat by teasing it apart and analysing different parts that seemed to differ in composition. I used hair (medullary and epidermal patterns), teeth, claws, hoofs, and feathers to ascertain diet composition of a scat (Koppikar & Sabnis, 1976) . Data were compiled as frequency of occurrence and as whole scat equivalents (Angerbjörn, Tannerfeldt, & Erlinge, 1999) .

I prepared reference slides from the hair samples obtained either from the dead prey or from the repository of Research laboratory Wildlife Institute of India of all the potential prey species in Kanha tiger reserve. Prey remain from the scats like hair, claws and bones were washed in the water than rinsed in distilled water and dehydrated in 90% ethyl alcohol. Identification slides were prepared from the hair samples obtained from scats, than it was compared with reference slides. The prey species were identified through hair medullary pattern, cortex pigmentation and relative size of hairs (Mukherjee, Goyal, & Chellam, 1994). The sample size (number of scats) was adequate as recommended in Ramesh et al (2009), and Lovari et al (2014). Prey availability was estimated through line transect (Jhala et al., 2014; Awasthi et al., 2016). I took ¾ of mean weight of female prey from the literature i, e. Schaller et al (1977), Wegge et al. (2009) and Awasthi et al (2016) as biomass of prey. I calculated biomass consumption through the model developed by Chakrabarti et al. (2016): $y = (0.033 – (0.025 \exp(-4.284x/PBW)))* PBW$ where y is biomass of prey consumed per scat and x is prey biomass and PBW is the predator biomass. I used the dietary niche overlap by using Pianka's index (Pianka 1973), the measure ranges from 0 (no common prey) to 1 (complete overlap).

5.3 Results:

Spatial Partitioning:

I found that at tiger home range scale (10 km^2 grids), leopards achieved high density in areas with medium or declining tiger density. Leopard populations showed growth in areas with low to medium-stable tiger density or declining tiger density (Figure 5.2). Density estimates of different management strata core and buffer zones of the Kanha tiger reserve: Sex-specific heterogeneity on g0 and σ were chosen over null model (Table 5.1) for both tiger and leopard. There was significant difference (at 95%CI) in densities between core and buffer zones of Kanha tiger reserve for both the species (Figure 5.3). Sex ratio was male biased in the multiple use buffer zone for the tigers but leopards sex ratio was female biased in both the zones (Table 5.2). The quantile regression results elucidate that tiger densities was significantly declined from 0.75th to 0.99th quantiles with the increasing distance from PA (Figure 5.5, Table 5.3).While the leopard densities has did not shown any significant relation with increasing distance from PA.

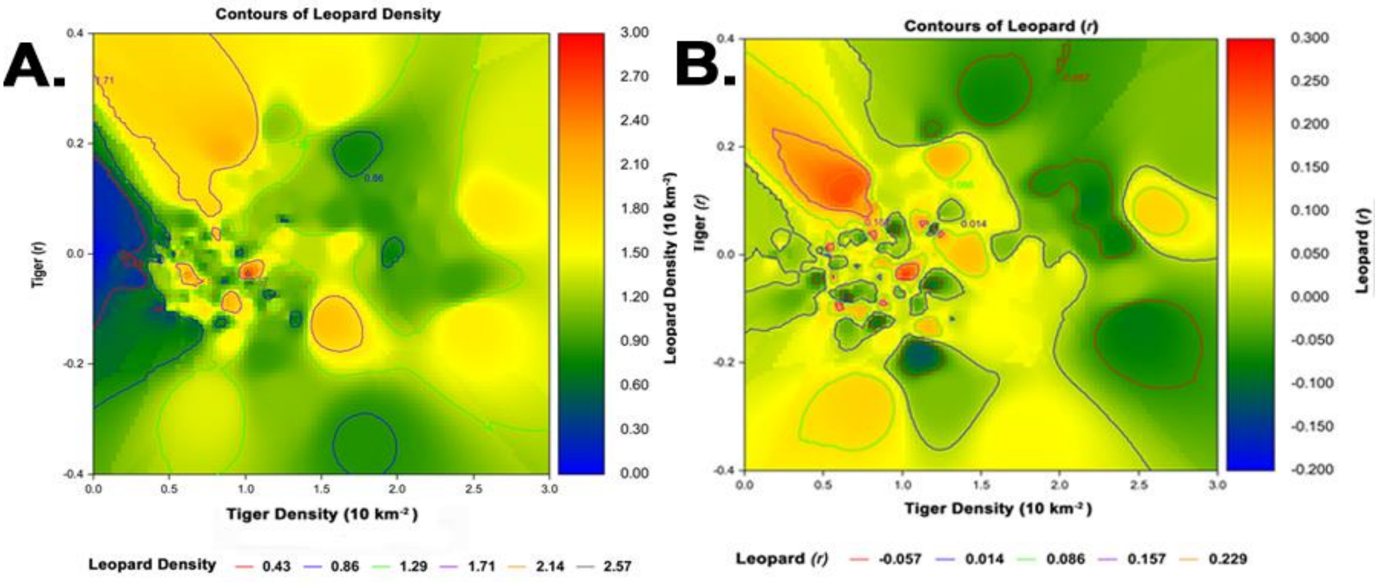

Figure 5. 2: Response of leopards (A) density and (B) realized growth rate (r) to tiger density and tiger growth rate at the scale of 10 km2 (home range size of female tigers) in Kanha National Park between 2013 to 2016; Growth in the leopard densities reported in medium and declining tiger densities while high leopard densities in low-medium and stable tiger densities area.

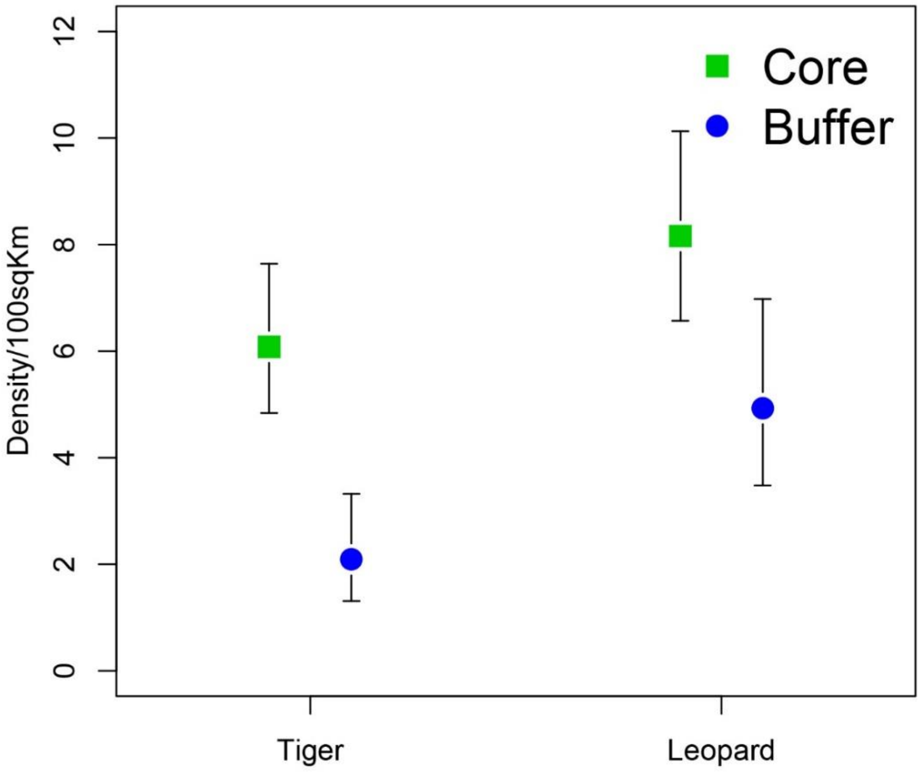

Figure 5. 3: Predator density in different management zones of Kanha Tiger Reserve.

Table 5. 1: Model selection parameters for both tiger and leopard at Kanha tiger reserve.

Species	Buffer zone				Core zone				Entire Tiger reserve			
	Models	***npar***	**AIC**	**ΔAIC**	**Models**	***npar***	**AIC**	**ΔAIC**	**Models**	***npar***	**AIC**	**ΔAIC**
Tiger	g_0~sex σ~ sex *pmix*~ sex	6	924.96	0.00	g_0~sex σ~ sex *pmix*~ sex	6	3215.46	0.00	g_0~sex σ~ sex *pmix*~ sex	6	4436.94	0.00
	g_0~1 σ~ sex *pmix*~ sex	5	925.81	0.85	g_0~1 σ~ sex *pmix*~ sex	5	3217.39	1.93	g_0~1 σ~ sex *pmix*~ sex	5	4443.52	6.58
	g_0~sex σ~1 *pmix*~ sex	5	928.59	3.63	g_0~sex σ~1 *pmix*~ sex	5	3324.70	109.24	g_0~sex σ~1 *pmix*~ sex	5	4634.56	197.62
	g_0~1 σ~1 *pmix*~ sex	4	940.61	15.65	g_0~1 σ~1 *pmix*~ sex	4	3380.07	164.62	g_0~1 σ~1 *pmix*~ sex	4	4728.55	291.61
	g_0~b σ~1 *pmix*~ sex	5	942.61	17.65	g_0~b σ~1 *pmix*~ sex	5	3382.07	166.62	g_0~b σ~1 *pmix*~ sex	5	4730.55	293.61
	g_0~b σ~b *pmix*~ sex	6	944.61	19.65	g_0~b σ~b *pmix*~ sex	6	3384.07	168.62	g_0~b σ~b *pmix*~ sex	6	4732.55	295.61
Leopard	g_0~sex σ~1 *pmix*~ sex	5	487.03	0	g_0~sex σ~ sex *pmix*~ sex	6	6843.58	0	g_0~sex σ~ sex *pmix*~ sex	6	7535.72	0
	g_0~sex σ~ sex *pmix*~ sex	6	487.94	0.9	g_0~1 σ~ sex *pmix*~ sex	5	6867.22	23.6	g_0~sex σ~1 *pmix*~ sex	5	7549.03	13.3
	g_0~1 σ~1 *pmix*~ sex	4	492.54	5.5	g_0~1 σ~1 *pmix*~ sex	4	6881.59	38.0	g_0~1 σ~1 *pmix*~ sex	4	7553.73	18.0
	g_0~1 σ~ sex *pmix*~ sex	5	494.42	7.4	g_0~sex σ~1 *pmix*~ sex	5	6881.86	38.3	g_0~1 σ~ sex *pmix*~ sex	5	7554.14	18.4
	g_0~b σ~1 *pmix*~ sex	5	494.54	7.5	g_0~b σ~1 *pmix*~ sex	5	6883.59	40.0	g_0~b σ~1 *pmix*~ sex	5	7555.73	20.0
	g_0~b σ~b *pmix*~ sex	6	496.54	9.5	g_0~b σ~b *pmix*~ sex	6	6885.59	42.0	g_0~b σ~b *pmix*~ sex	6	7557.73	22.0

Table 5. 2: Density (at 100 km-2), detection probability (g0), spatial scale of detection (σ km), and detection corrected sex ratio of tigers and leopards in two management zones of Kanha Tiger reserves in 2014.

Year	**Species**	**Models**	**Density** ± SE **(#/100 km^2)**	$g_{0\ Male}$ ± SE	$g_{0\ Female}$ ± SE	σ_{Male} ± SE (Km)	σ_{Female} ± SE (Km)	**Sex ratio (*pmix*) In proportion (Male: Female)**
2014	Tiger	Buffer Zone	2.09 ± 0.50	0.02 ± 0.005	0.06 ± 0.01	2.4 ± 0.27	2.3 ± 0.24	0.54 : 0.46
		Core Zone	6.08 ± 0.71	0.03 ± 0.002	0.05 ± 0.002	2.11 ± 0.53	1.72 ± 0.36	0.47 **:** 0.53
		Entire Kanha TR	4.50 ± 0.52	0.03 ± 0.002	0.05 ± 0.002	2.05 ± 0.5	1.81 ± 0.03	0.51: 0.49
	Leopard	Buffer Zone	4.94 ± 0.88	0.02 ± 0.003	0.02 ± 0.003	3.07 ± 0.30	1.99 ± 0.23	0.32: 0.68
		Core Zone	8.16 ± 0.90	0.02 ± 0.001	0.02 ± 0.003	2.15 ± 0.07	1.14 ± 0.06	0.39: 0.61
		Entire Kanha TR	7.71 ± 0.73	0.015 ± 0.001	0.021 ± 0.002	2.98 ± 0.096	1.32 ± 0.05	0.36 : 0.64

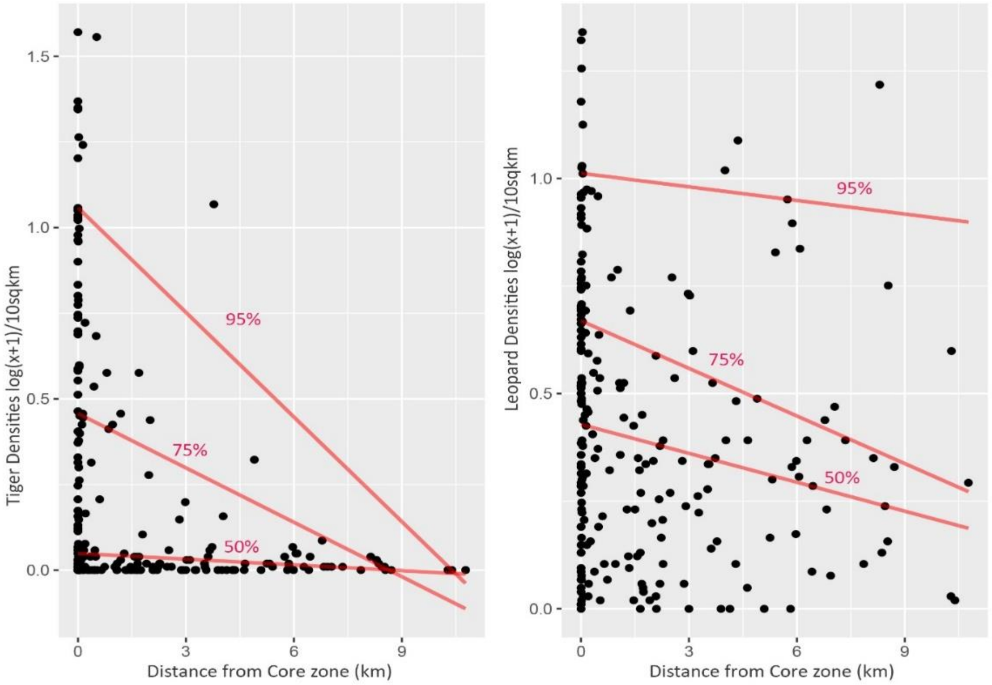

Figure 5. 2: Scatter plot and quatile lines (0.5, 0.75 & 0.95)between Predator densities vs Distance to Core Zone.

Table 5. 3: Quantile regression coefficients of tiger and leopard densities with increasing distance to PA (core zone)

Quantiles (tau)	**Tiger (Coeficients ±95%CI)**	**Leopard(Coeficients ±95%CI)**
0.20	0	-0.008 (-0.013 to 0.012)
0.50	-0.006 (-0.007 to -0.004)	-0.022 (-0.042 to -0.008
0.75	-0.07 (-0.07 to -0.053)	-0.042 (-0.05 to 0.007)
0.90	-0.09 (-0.11 to -0.08)	- 0.021 (-0.034 to 0.011)

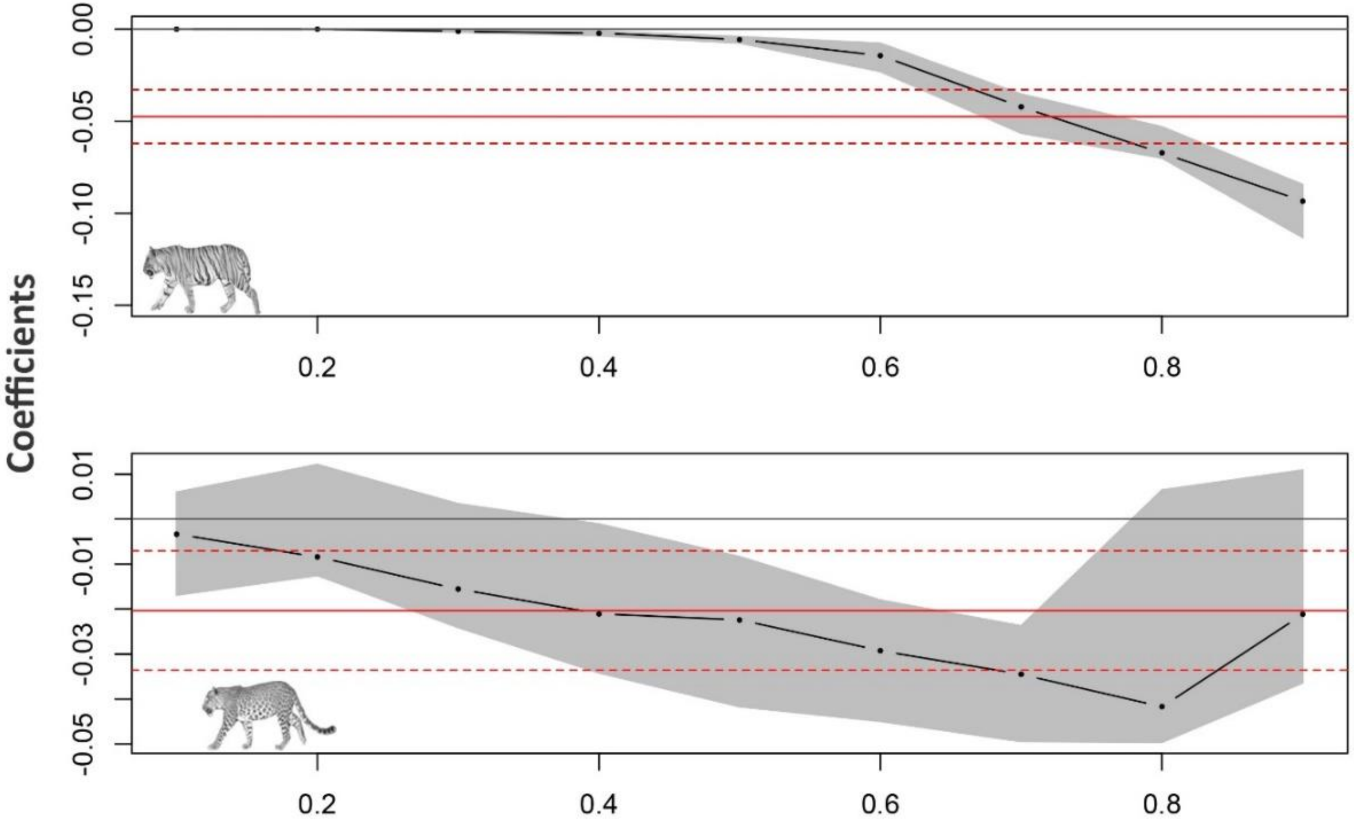

Figure 5. 3: Quantile Regression with PA distance and Carnivore Densities.

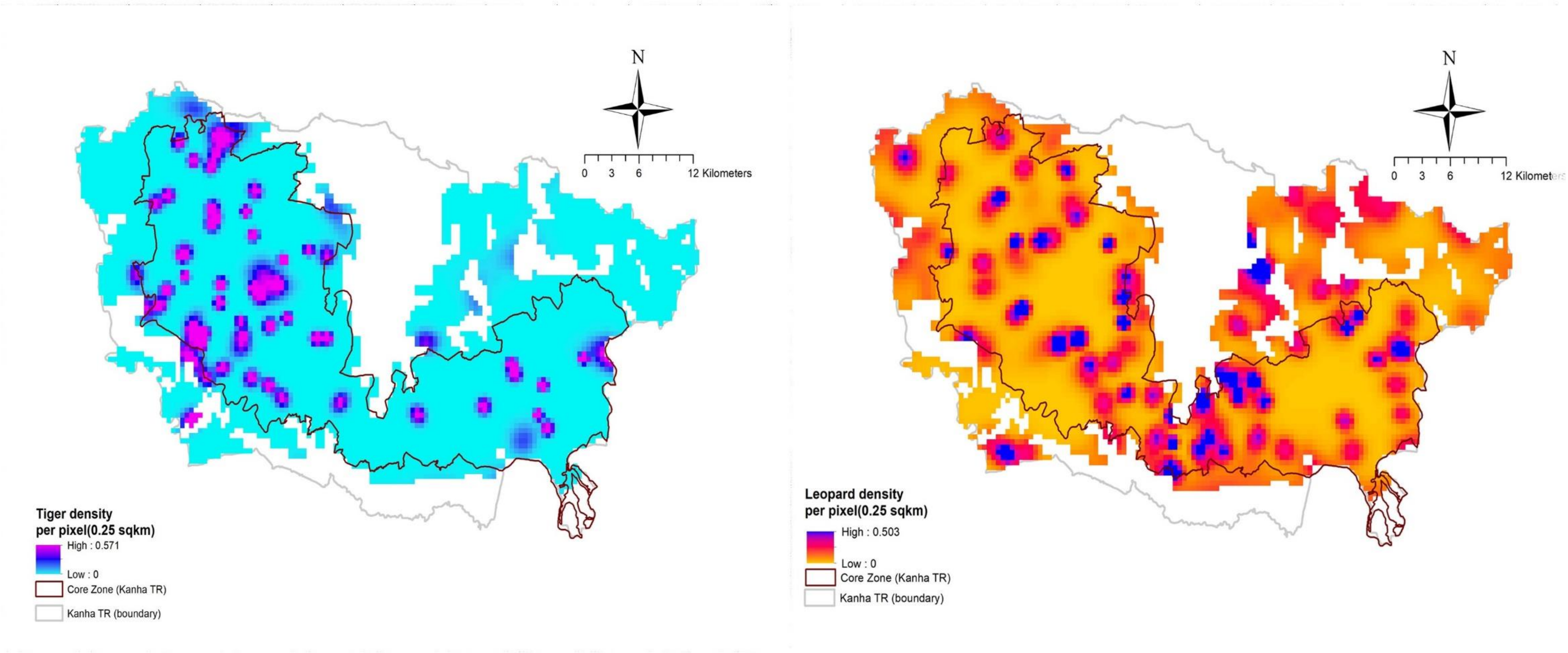

Figure 5. 4: Spatial Densities of Tiger and Leopard in Kanha Tiger reserve.

Temporal partitioning:

Tigers and leopards were primarily nocturnal. The activity overlap between tiger and leopard was 86% ($CI_{95\%}$ range 83 -89). Their diurnal activity was more in the core area compared to buffer area (Figure 5.7).

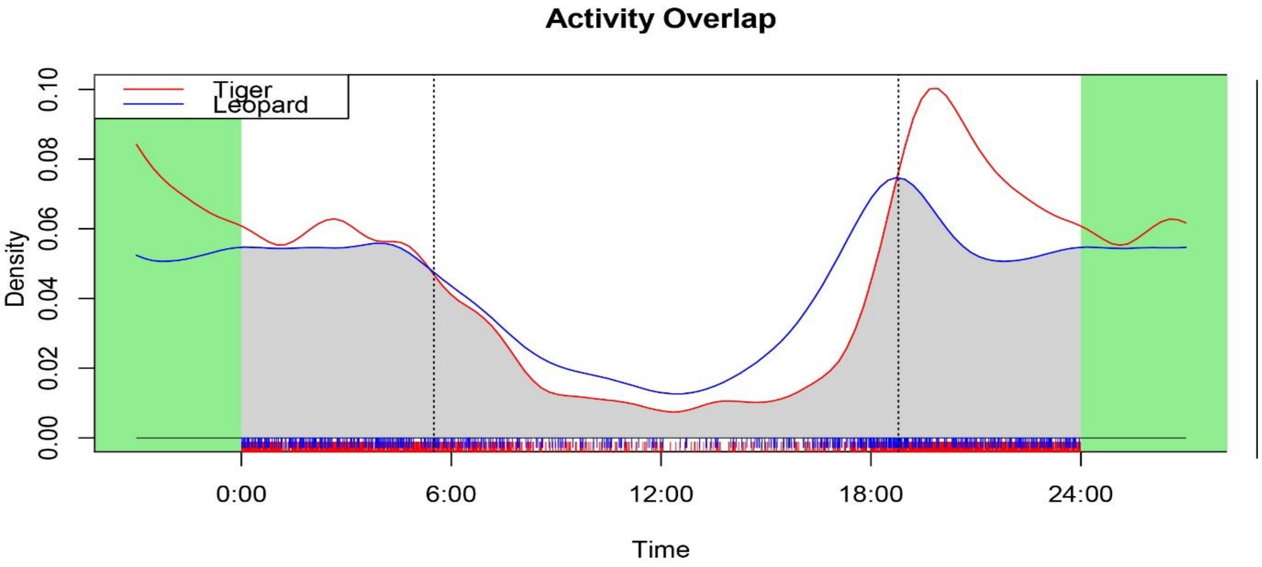

Figure 5. 5: Activity overlap of tiger and leopard in 24hrs day cycle.

Diet composition and overlap:

The total wild prey (ungulates, langur and peafowl) biomass availability was 6148.5 ± 49.8 kg/ km^{-2} (Table 5.4) (Jhala et al., 2014; Awasthi et al., 2016) . Wild prey dominated the diet of both tiger and leopards. For tiger diet the maximum contribution was of chital followed by sambar>wild pig = gaur > langur > cattle > barasingha (Figure). Chital was also major diet for leopard followed by langur > cattle > wild pig = gaur (Figure 5.8). The diet overlap between tiger and leopard was 94 % (Pianka, 1973).

Table 5. 4: Prey Densities in Kanha Tiger reserve.

Data from Awasthi et al. (2016), * Data from Jhala et al. (2014)

Species	No. of observation	Average cluster size	Group Density	Density Estimate	3/4th Body weight (kg)
Barasingha#	32	15.9 ± 3.54	0.10 ± 0.03	1.59 ± 0.70	109
Chital#	357	9.62 ± 0.52	3.14 ± 0.48	30.3 ± 4.9	47
Chowsingha#	8	1.39 ± 0.26	0.06 ± 0.02	0.09 ± 0.04	14
Gaur#	102	5.25 ± 0.63	0.92 ± 0.21	4.83 ± 1.25	561
Langur*	446	8.60 ± 0.34	7.18 ± .53	61.8 ± 5.20	10
Peafowl*	74	1.68 ± 0.12	0.79 ± 0.14	1.68 ± 0.12	3
Sambar#	250	2.86 ± 0.10	2.76 ± 0.33	7.90 ± 0.99	136
Wild pig#	91	4.94 ± 0.53	1.0 ± 0.15	5.29 ± 0.95	27

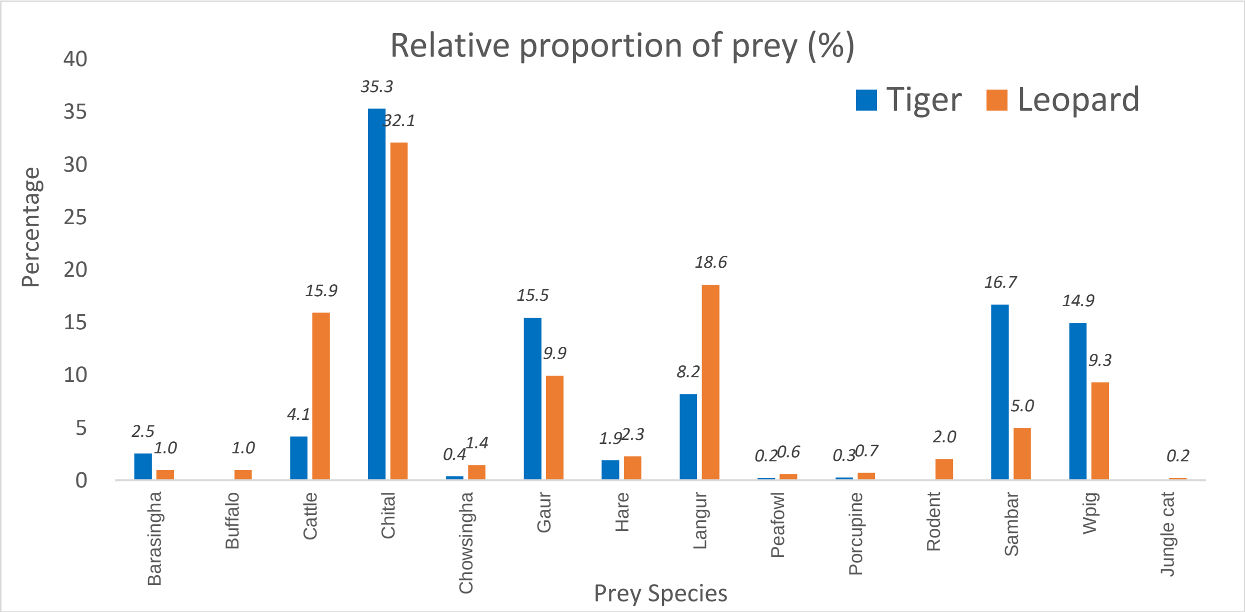

Figure 5. 6: Prey composition in the diet of Tiger and Leopard in Kanha tiger reserve.

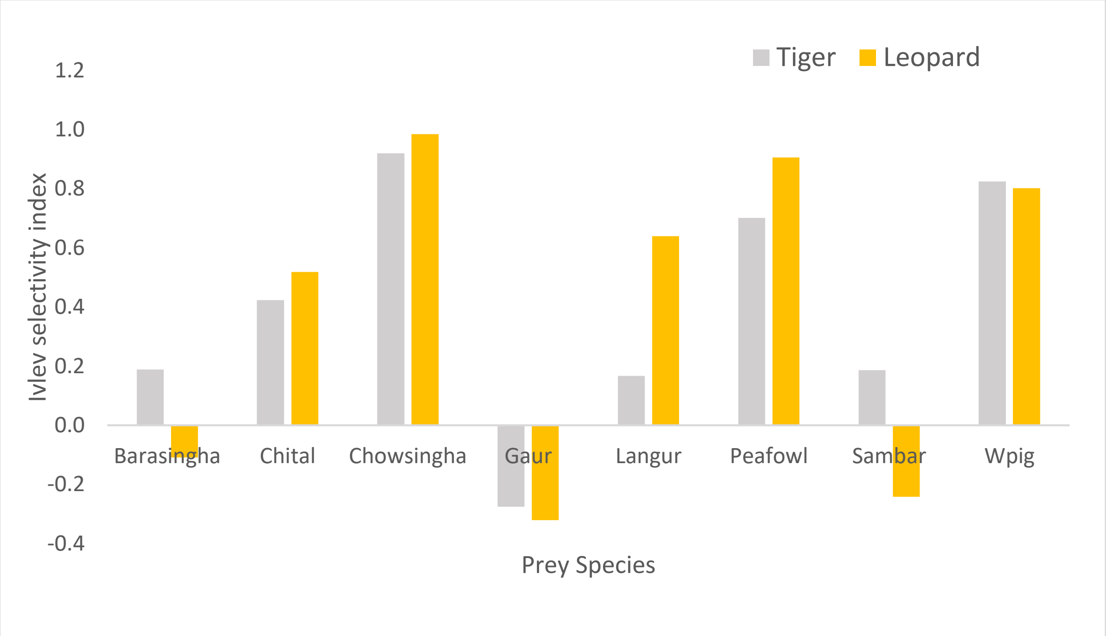

Figure 5. 7: Ivelev selectivity index of prey items in tiger and leopard diet.

5.4 Discussion:

This study provides an understanding of the likely mechanisms that permit coexistence of tigers and leopards in the Kanha tiger reserve.

Spatial partitioning:

The contour plots show that though leopards coexisted with tigers, they paid a price for this coexistence and achieved high-density populations only in areas that had either low tiger numbers or where tiger populations showed declines. Growing leopard populations were found in low tiger density areas or areas with declining tiger density (Figure 5. 2). This population response (regions with high leopard density and growth) show the costs associated to leopards for living sympatrically with tigers. Although I found higher densities of both the carnivores within the protected area but tiger densities steeply declined with the increasing distance from protected area, leopards, known to be better adapted to survive near humans use buffer zone without exhibiting density declines as seen in tigers.

The spatial density map (Figure 5.6) indicates that tiger and leopard spatially segregate themselves, factors responsible for high tiger density e.g. good prey, less disturbance were also good for leopard, however, and leopard densities were observed to be high only in pockets between high tiger densities –showing a clear pattern- suggesting that high tiger densities were detrimental to leopard. Sex ratio in large carnivores is female biased. The male skewed sex ration for tigers in the buffer indicates that this was suboptimal habitat for breeding females and used more by ousted or dispersing males.

The human use buffer zones and park periphery provides refugia for leopards from tigers since tiger densities were low in these areas. The spatial segregation between tiger and leopard was reported by (Seidensticker, (1976) and Steinmetz, Seuaturien, & Chutipong, (2013) while some studies reported complete spatial and temporal overlap (Karanth & Sunquist, 2000; Azlan & Sharma, 2003; Ramesh et al., 2012).

Temporal partitioning:

Since both carnivores, exhibit high nocturnal activity, hence, there is high temporal overlap between them. Earlier studies in India also did not report temporal segregation in activity between tiger and leopard (see Karanth & Sunquist, 1995; Ramesh et al., 2012). Since both the species are ambush predators they likely to utilize the evening and night hours for hunting.

Diet composition and overlap:

Although the diet of both the carnivores had considerable overlap and the principal prey was chital for both the carnivores since chital was the most available prey. The highest composition of chital followed by sambar in the diet of tiger was comparable to earlier studies (Chital 52.2% and sambar 10.4 %) within Kanha tiger reserve by Schaller (1967).Gaur and wild pig were found to be the next most fed prey of tigers (Figure 5.8). Leopard being a generalist predator fed on diverse prey species. As reported by Schaller (1967) within this study area the next most fed prey of leopard was langurs, which also corroborates with this study and in Nepal by (Lovari et al., (2015).The results of leopard diet suggests that cattle contributed as the third most utilized prey. Since high leopard densities mostly spaced out near to periphery and human settlements (Figure 5.6), which may result in high cattle predation(Odden & Wegge, 2009). The Ivlev selectivity index (Figure 5.9) and diet composition suggests that tiger preferred high to medium sized prey(Chital-Sambar) while leopard concentrate more on small body sized prey(Chital-langur) however the contribution of largest ungulates gaur in leopard diet indicates that leopard likely to predate on gaur fawn or scavenge on the gaur killed by tigers.

I could not distinguish the age and sex of the prey item nor between scavenging and predation. It is likely that tigers take adults of the same prey while leopards predate young as well as scavenge off tiger kills. As reported from the studies from southern India, tigers used to feed on large-sized prey, while leopard prefer to predate on small to medium sized prey(Karanth & Sunquist, 1995; Andheria, Karanth, & Kumar, 2007). Possibly this behavioural adaptation in prey selection had developed to avoid competition and facilitate coexistence(Connell, 2006).

The mechanism of diet overlap and coexistence is related to high and diverse prey availability in Kanha tiger reserve, which is likely to be associated with habitat heterogeneity. The heterogeneous habitat with ample prey facilitates coexistence between these two carnivores.

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