POPULATION DYNAMICS AND RESOURCE SELECTION BY TIGERS IN CORBETT TIGER RESERVE

A THESIS
Submitted by

SHIKHA BISHT

for the award of the Degree of

DOCTOR OF PHILOSOPHY
IN
(WILDLIFE SCIENCE)

Under the guidance of
(Y.V JHALA& QAMAR QURESHI)

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JULY- 2019

Declaration by the Candidate

I declare that the thesis titled “Population Dynamics and Resource by Tigers in Corbett Tiger Reserve” submitted by me for the degree of Doctor of Philosophy is the record of research work carried out by me during the period from 2010 to 2016. Under the guidance of Y.V. Jhala and Qamar 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.

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Executive Summary

Large carnivores are on the brink of extinction across most of their range and this is especially true for tigers, that are symbolic of the wilderness of the Asian forests. India is the stronghold for tigers in the world but their distribution is restricted to patches in a landscape. Largest tiger populations, not only in India but also in the world, are found in the Western Ghats (Karanth et al 2006), in the mangroves of the Sunderban (Roy et al. 2015) and in the western Terai landscape of Corbett (Bisht et al 2019). Among these the densest population of tigers is found in Corbett, but information on vital rates such as survival, recruitment, reproductive potential, along with space use and food habits of tigers from such a system are not known.

The overarching goal of my study was to use camera trap based capture mark recapture (CMR) technique to understand the population dynamics and space use by tigers in this high density tiger population. For this I camera trapped 521 km^2 of Corbett National Park (CNP) under open population capture–mark–recapture framework between 2010 and 2015 to estimate annual abundance, spatially explicit density, survival, recruitment, temporary movements, sex ratio and proportion of females breeding. In 6 years, we recorded 6,202 photo-captures of 307 individual tigers. Annual tiger abundance and density were stable at 120 (SE 19) and 14 (SE 3) per 100 km^2 respectively. Detection probability of tigers was 0.18 (SE 0.03) and detection-corrected male:female sex ratio was female biased (0.80 SE 0.13). Apparent annual survival probability was 0.79 (SE 0.05) for females and 0.60 (SE 0.04) for males. Survival of tigers in CNP (0.68 SE 0.12) was lower than that reported for other populations. CNP tigers showed high reproduction with 54.8

(SE 5.1) % females breeding and with addition of 35 (SE 8) % as new recruits to the population each year.

Like the current study, monitoring programs are dependent on a robust sampling methods since inferences on population growth or decline are very important for management of a protected area and are sensitive to the assumptions of the sampling method. As part of the current study we tested the effect of sampling days on the estimates of abundance in a closed CMR study. We camera trapped an area of 100 km^2 for one year continuously and obtained 1940 photographs of 26 tigers in 18,475 trap-days. We estimated abundances for increasing sampling windows (15-90 days) by iterating closed CMR analysis from 50 random start occasions for each window. Tiger abundance increased asymptotically from 15 to 22 and precision increased from 22 to 7 % CV with increasing sampling window. The increase was drastic between 15-45 days (15% per day) compared to 45-90 days (4% per day). We used open Robust Design models (Pradel and Pollock) on primary periods of 24 days, along increasing interval between two sampling periods (0-90 days) to examine how enlarging the sampling window influences detection probability and demographic parameter estimates. Small sampling windows (<30days) positively biased detection probability as individual heterogeneity in capture rates could not be accounted for; yielding negatively biased estimates of abundance (-27% bias). Recruitment rate (new adults at time t per adult at t-1) and apparent mortality (1-S) increased with sampling window; indicating that population change (additions + deletions) increased from 2% (48 days) to 18% (120 days). Although temporary emigration rate was constant across sampling windows (~11% between 48-120 days), temporary immigration rate increased abruptly from 18% (48-60 days) to 86% (60-120 days);

indicating that violation of geographic closure cannot be completely avoided and can bias the abundance estimate if the sampling extends beyond 60 days. We suggest using the sampling window suggested here to optimize the trade-off between unbiased detection probability estimation ($\geq$25 days) and tolerable levels of individual turnovers (5% in $\leq$ 60 days).

Most of our knowledge on space use and food habits of tigers in India comes from the tropical deciduous forests of western ghats and central India. We looked at space use and food habits of tigers in Corbett, which has high competition for space, high turnover and also high reproductive potential. Cervids accounted for 90% of the tigers diet and Chital (*Axis axis*) was the preferred prey. We used camera trapped based minimum home range estimates for resident male and female home ranges, shifts, expansions/contraction and overlaps. Home range of males (n=15) 16.4 ± 1.6 km^2 was 5 times more than the home range of females (n=14, 3.9 ± 0.8 km^2). None of the resident females showed shifts in its home range area while 4 of the males, 2 of them sub adults, showed shifts and home range expansion between 2010 and 2015. We found relatively high overlap between females (16%) than reported by other studies and males had an average overlap of 34%. Smaller annual minimum homerange usage areas of the breeders/residents and high female home range overlap than those reported for tigers (see Sunquist 1981, Simchareon *et al.* 2014 and Chundawat *et al.* 2016) suggests adjustment in space in response to high competition in CNP.

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This study is culmination of 8 years of my research journey in the forests of Shivaliks. Deploying hundreds of camera traps, walking scores of line transects and going through thousands of camera trap images and putting all of it in order has been the major part of my life since 2010. For this journey I would like to thank several people, who have advised, encouraged and supported me. First and foremost, my parents, who have been supportive and patient even though they don't understand much of my work. A special thanks to my mom for being such an independent human and for the way she raised us siblings. A big thank you to Sutirtha, for his advice, help and commitment in both professional and personal life. I would have done all this without him, but not as well as I did with him by my side :)

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CHAPTER 1: INTRODUCTION

Tiger (*Panthera tigris*) is an icon of conservation and embedded in the culture of India. Tigers need large undisturbed habitats with adequate prey base to persist which makes it an ideal umbrella species for conservation of forested ecosystems. The size and extent of the protected areas in India is a major concern towards long-term persistence of tigers since most of the protected areas are too small to harbour demographically and genetically viable populations. The problem of size can be overcome by maintaining a meta-population framework of tiger populations, wherein, Tiger Reserves and surrounding Protected Areas (hereafter PAs) serve as local populations connected by the intervening forested corridors (Wikramanayake et al. 2011). Through natural movement and dispersal of tigers, the long-term persistence of the meta-population is enhanced (Hanski 1991)

Corbett Tiger Reserve (hereafter CTR) along with Rajaji Tiger Reserve (hereafter RTR) and its adjoining forests forms one such habitat. It is one of the largest contiguous tiger habitat (7500 km^2) in north-west India, and a level I Tiger Conservation Unit (highest priority globally, hereafter TCUI, Wikramanayake et al., 1998). Towards its west lies RTR and in its east lie Dudhwa Tiger Reserve in India and Suklaphanta Wildlife Sanctuary (WLS) and Royal Bardia National Park in Nepal, along with their adjoining forests forming a contiguous network of populations. Together they form the western Terai Arc Landscape (hereafter TAL). The CTR population serves as an important source population for the western TAL since tigers from this source can potentially disperse both eastwards, through the

Kosi River corridor connecting CTR to Ramnagar-Terai-Haldwani-Pilibhit Forest Divisions, and westwards, through the Lansdowne Forest Division and Sonanadi Wildlife Sanctuary to RTR. These corridors are the only linkages for gene flow across TAL. Owing to its size, extent and function, CTR population is likely the critical determinant for the long-term persistence of tiger in TAL and should be prioritized for research and conservation.

The country-wide tiger monitoring exercise has identified CTR as a high tiger density area (19 ± 0.54 per 100 km^2 in 2006-07, Contractor 2007; Jhala et al. 2011). Tiger occupied area in the extended landscape (CTR and Lansdowne, Kashipur, Ramnagar, west Haldwani, north-west Nainital and lower Ranikhet) has increased from 1524 km^2 to 2287 km^2 from 2006-07 to 2010-11 (Jhala et al., 2011). Estimated tiger numbers have also increased from 161-195$_{95\%CI}$ (Jhala et al., 2008) to 190-239$_{95\%CI}$ (Jhala et al., 2011). But these studies are based on snapshots of the population at discrete times, and do not provide further insight into tiger ecology required to keep a pulse on the health of the population as well as for understanding the mechanisms operating in the system so vital for long-term persistence.

Distribution and abundance of species usually fluctuate over long time periods (Gaston 1994) and much of applied ecological research revolves around understanding these patterns and their processes. Birth, immigration, death and emigration are the drivers of population change over time and information on these life-history parameters and their complex interplay determines the net population change (Williams et al., 2002) which is crucial from conservation perspectives. Characterising a population in terms of its demographic parameters helps understand population responses and the role of conservation management in the landscape; and are important parameters for any population viability predictive analysis for the future of the population. Also, distinction between demographic groups is important, as they contribute differently to the long-term viability, understanding which group should be targeted for management. Long-term life-history monitoring is, hence, necessary to understand the nature and scale of population fluctuations in order to make informed management decisions (Gibbs et al., 1998).

Given the importance of population dynamics, relatively few studies on solitary large carnivores have been carried out (but see Lambert et al 2006 for Cougar (*Puma concolor*), Mondal et al 2012 for Leopard (*Panthera pardus*), Sharma et al. 2014 for Snow Leopard ((*Panthera uncia*), Harmsen et al. 2017 for Jaguars (*Panthera onca*)) because of their long lifespan, large home ranges, and elusive nature. In case of tigers, a few studies, in Nepal (Sunquist 1981, Smith 1993, Kenny et al., 1995), India (Karanth et al., 2006, Sadhu et al., 2017, Chanchani 2016, Majumdar et al., 2012), Russia (Kerley et al. 2003) and Malaysia (Dungachistatri et al. 2016) have generated estimates of survival rates and land tenure system based on radio-telemetry of 30-40 individuals and/or camera trap based mark-recapture (CMR). In most monitoring cases, abundance/density, and not life-history, has been the central parameter of interest estimated by CMR (Karanth 1995, Karanth&Nichols 1998, 2000 & 2002, Karanth et al., 2004, Kawanishi & Sunquist 2004, Wegge et al., 2004, Simcharoen et al. 2007, Lynam et al., 2009, Trolle & Kery 2003), radio telemetry, and sign surveys (Johnsingh & Negi 2003, Jhala et al. 2011). In case of the Indian Terai the picture is grimmer, with only two other long term study (Harihar 2013 and Chanchani 2016) on tigers where only Chanchani 2016 estimate demographic parameters from 3 years of camera trap data. Chanchani 2016 found that tiger occupancy and abundance was similar or higher in multiple use forest, that have high human use, than in several protected areas. Both Harihar 2013 and Chanchani 2016 find that key predictors for tiger distribution were distribution and abundance of prey and some key habitats like the tall grasslands in case of central Terai and presence/absence of human use in Western Terai. In both western and central terai habitat connectivity promoted high occupancy only when forests connected by corridor are well protected and additionally in western terai are devoid of human disturbance. These study identified ecological and anthropogenic factors that enable tiger persistence in the multiple use forest system central terai. Although vital rates were estimated by Chanchani 2016, the duration of the study (3 years) were less than that required to robustly estimate survival, movements from camera trapped based CMR (Gerber et al. 2014), while in the western TAL these estimates are missing altogether.

Resource choice is a hierarchial behavioural response to environmental factors shaped by evolutionary and ecological processes (Cody 1985). Adequate quantities of usable resources are necessary to sustain animal populations (Manly et al., 2002) and their differential use allows species-coexistence (Rosenzweig 1981). For these reasons, ecologists have always attempted to describe and understand space use by animals (Horne et al., 2008). Space use is primarily influenced by i) the tendency to remain in a particular area or home range for site-fidelity or territoriality (Burt 1943), ii) the distribution of selected/required resources (Bergerud 1974), and iii) the location of other animals (e.g., mates, competitors and prey; Wauters et al., 2000, Horne et al., 2008).

Placement of home ranges(and therefore access to resources) in mammalian species is influenced by social interactions between individuals (Carpenter & MacMillen

1976, McLoughlin & Ferguson 2000). In solitary carnivores, females are predicted to be natal philopatric; establishing home ranges close to their place of birth (Waser & Jones 1983), while males are the dispersing sex and establish ranges away from their natal areas (Schaller 1967, Sunquist 1981, Smith et al.1987). Habitat attributes, such as food supply (Karanth & Stith 1999, Karanth et al., 2004) or access to refuges, often influence home-range size in tigers. Such qualitative differences in habitat attributes usually lead to conspecific competition over space, determining the distribution of individuals within populations. Sunquist (1981) and Smith (1993) reported patterns of resource dispersion to determine home-range size in tigers.

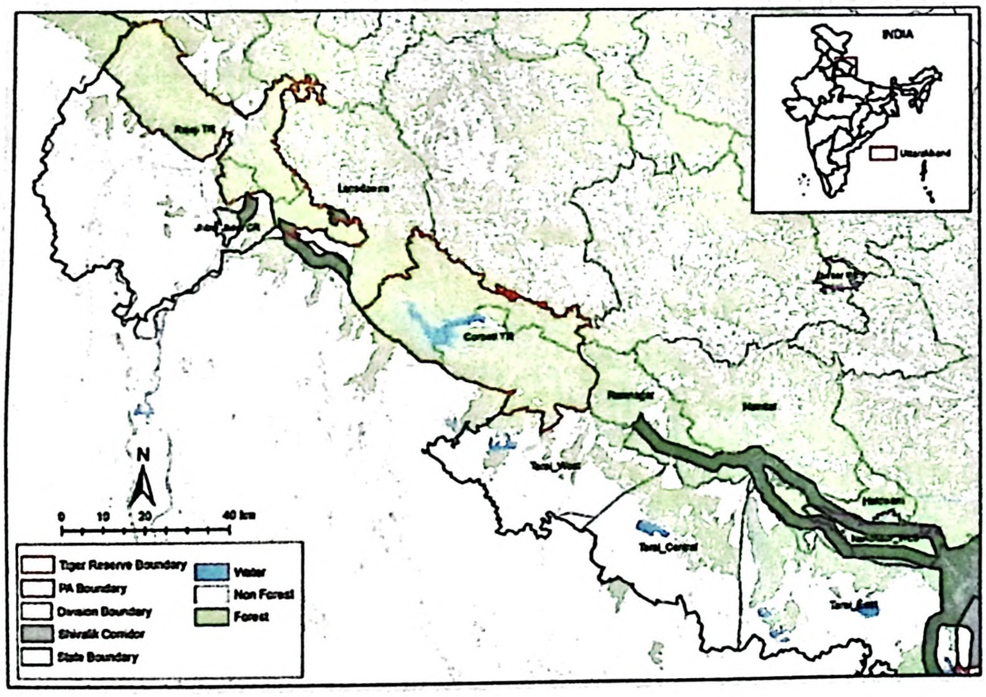
In this context the current study proposes to 1) monitor tiger abundance over time for population trend and using intensive camera trapping data look at effect of sampling duration on these estimates, 2) characterise life history parameters (such as survival, temporary movement, recruitment and reproductive potential) for biological understanding of tiger population dynamics , 3) estimate resource choice in terms of prey and 4) understand spatial organisation of tiger individuals in the population from shifts and overlaps of individually occupied areas. I look at population dynamics of tigers in Corbett which is the most important population of tigers in TAL, a global priority landscape for tiger conservation. I use six-year data on tiger demography to estimate survival, temporary movement, recruitment, growth rate, population trend and reproductive potential of the single largest tiger population in the world. This first ever demographic study of tigers in Western Terai helps to assess and establish importance of a large source population in a landscape for long-term persistence of tigers and to gain insights into the spatial organisation that enables such high density tiger population to persist.

CHAPTER 2: STUDY AREA

2.1. Location

Popularly known as the land of trumpet, roar and song, Corbett National Park (CNP) is situated in the foothills of the Himalayas i.e. the Shivalik range. CNP falls within Nainital and Pauri Garhwal districts of Uttarakhand (Figure 2.1). The total area of the Corbett Tiger Reserve is 1288.32 sq. km. It comprises of 520.82 sq. km of National Park, 301.18 sq. km of adjoining Sonanadi Wildlife Sanctuary and 466.32 sq.km of buffer zone (Barthari 1999). After undergoing various name changes it came to be recognized as Corbett NP after the hunter turned conservationist Jim Corbett in the year 1957. It houses a variety of endemic as well as endangered species and is perhaps their last refuge providing hope for their continued survival.

Figure 2. 1 Map of Study Area showing location of study area in the Uttarakhand, India. Also shown are the important forest division around Corbett Tiger Reserve along with forest corridors (Qureshi et al. 2015) that connect these forests



2.2. History

CNP was established on 8th August, 1936 and was the first national park not only in India, but in the whole of the Asian mainland (Bharthari 1999). In 1936 it was named Hailey NP after Sir Malcolm Hailey, the then governor of Uttar Pradesh, who was influential in creation of a 257 km^2 of protected forest in what used to be a common British hunting ground. Post-independence in 1954 it was named Ramganga National Park and finally it was rechristened as Corbett National Park in honour of Sir Edward James Corbett, the hunter-naturalist who later turned author and photographer and the man who facilitated the charting out of boundaries and establishment of the National Park. In 1973, with the help of World Wildlife Fund, Project Tiger was launched in CNP and it was one of the first such tiger reserves in the country. The area has increased from 257 km^2 to 520.82 km^2 in 1966 to compensate for the land submergence due to the creation of the dam at Kalagarh, which also serves as a perennial water source for animals in the park(Barthari 1999).

2.3. Geology/ Physical features

CNP lies in the Shivalik range situated in the outer foothills of the Himalayas and is composed of alluvial detritus material derived mainly from sub aerial waste from the Himalayan system (Pant 1986). The Himalayan Rivers bring coarse material which deposits immediately along the foothills forming a layer of boulders known as Bhabar. CNP is confined to the Bhabar tract of Shivalik formation with an altitude range of 350 –1050 meters (Pant 1986). It is characterized by hilly, undulating terrain with ridges and valleys and dry river beds with coarse boulders. The porous boulders are responsible for low water levels at the surface. This also leads to the disappearance of streams from the surface during the hot season only to re emerge following the first rainfall of the season. The topography is considerably varied with hilly and riverine areas, temporary marshy depressions, plateaus and ravines. A series of almost parallel ridges run from the North West to the South East decreasing in height on approaching the plains along the southern boundary. Conglomerates, sand rock, sand stone and bhabar deposits together contribute to the geological aspect of the park. The river Ramganga and its tributaries are the primary source of water in the park. The reservoir formed due to the construction of the dam is 80 sq.km, out of which 42 sq. km falls within the park. The reservoir also proves to be a perennial source of water to the park. Kosi River flows along the eastern boundary of the park which also acts as a water source to CNP.

2.4. Climate

The general climate is tropical with three main seasons *viz.* winter from November to February, summer from March to June and monsoon from mid June to October (Bhartari 1999). Temperature ranges from 3°C in December – January to 42°C in May-June. Since the NP is situated in the densely forested Shivaliks, it remains fairly humid throughout the year. The South West monsoons are the main source of rainfall with maximum rainfall occurring from June to September.

2.5. Vegetation

The forests of Corbett NP are classified into three major forest types *viz.* Northern moist deciduous, Northern tropical dry deciduous and Himalayan sub tropical pine forest

(Champion and Seth 1968). 617 species of plants were reported by Pant (1986) out of which 594 were angiosperms, 1 species of gymnosperms and 22 species of ferns and fern allies. Upreti and Chatterjee (1999) recently added 69 species of lichens to the flora of CNP. Sal (*Shorea robusta)* is the most dominant tree species gregariously growing in the park area. Evergreen species like *Mallotus philippinensis* and *Syzygium cuminii* are also commonlyseen. Other medium sized evergreens include *Litsea monopetala, L.glutinosa,* and the fragrant *Murraya panniculata.* Among deciduous species *Terminalia alata, Terminalia chebula, Semicarpusanacardium, Lannea coromandelica, Sapium insigne, Lagerstormia parviflora, Buteamonsperma, Cassia fistula and Ehretia levis* can be seen throughout the park in good numbers. At several places *Bombax ceiba* and *Anogeissus latifolia* can be seen as Salassociates. *Phyllanthus emblica, Acacia catechu, Kydia calycina, Dalbergia sissoo* and *Holoptelia integrifolia* can be seen at open sunny faces near *sots* and lining grasslands. Plantations of *Tectona grandis* and *Eucalyptus spp* are present near the eastern and southern boundaries of the park. Commonly occurring shrubs are *Colebrookea oppositifolia, Glycosmis arborea, Murraya koenigii, Justicia adhatoda* and *Woodfordia fruticosa. Lantana camara and Cannabis sativa* are the most abundant weeds.

Vast sprawling grasslands are the characteristic of some areas of the park. The main grass species found in these grasslands are *Saccharum bengalenses, Themeda arundinacea, Arundo donax, Vetiveria ziznoides, Apluda mutica, Heteropogon contortus, Eragrostis spp.*and *Cynodon dactylon. Eulaliopsis binata* and *Thysanolena maxima* can be seen growing on cliffs and moist shady places.

2.6. Fauna

CNP supports a sizeable variety of faunal diversity (Lamba 1980). Other than the tiger (*Panthera tigirs)* the park supports felids like leopard (*Panthera pardus*), leopard cat (*Prionailurus bengalensis)* and jungle cat (*Felis chaus*). Other carnivores include the golden jackal (*Canis aureus*), sloth bear (*Melursus ursinus*) and Himalayan black bear *(Ursusthibetanus).* Herbivores include Elephants (*Elaphus maximus)*, sambar (*Cervus unicolor*), cheetal (*Axis axis*), barking deer (*Muntiacus muntjak*) and Hog deer (*Axis porcinus*). Nilgai (*Boselaphus tragocamelus*) is seen only in the disturbed fringes. Small Indian civet *(Viverricula indica*), Himalayan palm civet (*Paguma larvata*) common palm civet (*Paradoxurus hermaphroditus*) are found along with mustelids like yellow throated marten (*Martes flavigula)* and mongoose (*Herpestes spp*). Black napped hare (*Lupus nigricollisnigricollis*) and Indian porcupine (*Hystrix indica*) are of common occurrence. The Ramgangariver system also supports a good population of otters (*Lutra lutra, Lutrogale perspicillata*).

Among reptiles, a good population of Gharials (*Gavialis gangeticus)* and *Mugger (Crocodilus palustris*) can be seen in the river as well as the reservoir. Snakes like King cobra (*Naja bungarus*), cobra (*Naja naja*) and Python (*Python molurus*). Among other reptiles are the rock agama (*Agama spp*), Monitor lizard (*Various spp*) and various turtle species like *Lessimys punctata*, Indian black turtle (*Melanocheyis trijuga)* and Tricarinate hillturtle *(M. tricarinata)* (Bharthari 1999).

The avifauna of CNP is very rich. 549 species of resident and migratory birds have been reported from the park. Some of the noteworthy species occurring in the park are Greatpied hornbill (*Buceros bicornis*), Great slaty woodpecker (*Mulleripicus pulverulentus*), Khalijpheasant (*Lophura leucomelanos*), Himalayan griffon (*Gyps* *himalayensis*), Cinereous vulture (*Aegypius monachus*), collared falconet (*Microhierax caerulescens*), etc.

2.7. Human disturbance

There are no villages in CNP at the moment. Three villages were relocated in 1994from the southern boundary of the park after which the park has been free from human settlements. However, the villages of Dhara, Laldhang, Dhela as well as small *Gujjar* settlements like the one in Jhirna continue to enjoy rights within the forest blocks of the national park adjoining these settlements. Despite the clear demarcation of the core area boundaries through firelines, the villagers continue to move inside the core zone for collection of NTFP (Barthari 1999). CNP is immensely popular as a tourist location and draws considerable number of visitors each year. There has been tremendous growth in the number of privately owned resorts and hotels along the eastern boundary of the park cutting off the access of animals from the park to Kosi River flowing along the eastern boundary.

2.8. Tiger and other carnivore studies

Johnsingh and Negi 2003 carried out a landscape scale survey for tiger and leopard status in the Rajaji-Corbett Conservation Unit. The survey was carried out across 12 forest divisions between river ganga and river sharda and tiger and leopard status was evaluated through pugmark census. The study highlights the importance of Corbett in the long term persistence of tigers in the landscape and suggest a 2000 sq km area as Greater Corbett Tiger Reserve to be kept as inviolate as possible. Since then, All India Monitoring in 2007 (Jhala et al. 2008) estimated the tiger numbers in the park using modern scientific tools of camera trap based capture mark recapture. Contemporaneously, Contractor 2007 did her Masters dissertation on effect of trapping design on the estimates of population. Following this current project to monitor source population of titers in Corbett tiger reserve was taken up by WII and the state forest department (Bisht et al. 2012). The study aimed to monitor tiger and its prey population in the park annually. Corbett tiger population has been assessed annually since 2010 either as part of the above mentioned project or under the All India Monitoring exercise 2014 (Jhala et al. 2014) and 2017.

CHAPTER 3: ABUNDANCE, DENSITY AND GROWTH RATE OF TIGERS IN CORBETT TIGER RESERVE

3.1 Introduction

Monitoring a population over time provides information on patterns and processes behind observed fluctuations in its abundance and much of the applied ecological research is about understanding these patterns and processes (Gaston 1994). Estimating number of individual organisms in a population at a particular time is key to a monitoring program/ study, making abundance and density central parameters of interest. These parameters provide an objective measure of assessing trends in a particular population which is useful for wildlife management.

Monitoring large carnivore populations is a global challenge due to their large home-ranges, wide distribution, low density and cryptic nature. Along with this, long-term monitoring studies in India are fraught with multiple hurdles of funds and permissions to work.. Therefore, studies monitoring large carnivore population are mostly restricted to some sites and also very few in number. One of the largest monitoring program for any large carnivore takes place in the India for tigers (Jhala et al 2014). But this is a quadrennial survey on assessing tigers, its co-predators, prey and their habitat which provides a snapshot view of status of tiger populations. These studies are based on snapshots of the population at discrete times, and do not provide further insight into specific demographic parameters so vital for understanding mechanisms of population dynamics. Despite harbouring one of the largest single tiger population in the world there have been no long-term work carried out to understand the demographic parameters and mechanisms behind the observed trends in tiger numbers not only in Corbett National Park but also in the landscape. In comparison to Nepal Terai which has been intensively studied by several researchers for the since the 1970's (Seidensticker 1976, Sunqist 1981, Smith *et al.* 1989, Smith 1993, Tamang 1982, Smith *et al.* 1983, 1998, Smith & Mc Dougal 1991) and provide us information on land-tenure system and social organisation of tigers, very few studies on these aspects of tiger ecology have been conducted in India (but see Karanth et al 2006, Sadhu et al 2017, Majumdar et al. 2017). Johnsingh &Negi (2003) gathered information on status of tiger and leopard while also assessing the biotic pressures at a landscape level. Thereafter, Johnsingh *et al.* (2004) conducted a survey to determine status of the tiger in the region and to identify the existing corridors between Protected Areas. Since 2004, the Wildlife Institute of India has conducted study on population status, tiger's response to various disturbance regimes (Harihar *et al.* 2009) and tiger leopard interactions (Harihar *et al.* 2011) in Rajaji National Park. In 2007 Contractor conducted a short term study on evaluating camera trap design and sampling intensity for estimating tiger population in Corbett National Park. In Corbett, apart from camera trapping carried out under the All India Tiger Monitoring exercise in 2006-2007, 2009-2010 and 2013-2014 (Jhala *et al.* 2008, 2011, 2014), no other long-term study on tigers has been carried out. Current study aims to fill this gap in knowledge and provide annual abundance and density of tigers in Corbett from 2010-2015, along with the population growth trend of this population.

Till the advent of remotely triggered camera traps (in mid-1990's) placed at optimal locations in the forest to individually identify tigers from their stripe pattern (Karanth 1994), pugmark based method (Panwar 1979) was used to estimate the population of tigers in India. By being able to individually identify or "mark" an animal a suite of sophisticated and robust method of capture mark recapture (CMR) (Otis et al. 1978) could be applied to tigers for their abundance and density estimation. CMR techniques have also been used for estimating population parameters for fish, birds and small mammals (Seber, 1982) that could cannot be easily counted using line transect/point transect based distance sampling methods (Buckland *et al,* 1993). The theory and practice of capture-recapture methods started with the simplest Lincoln - Peterson estimator (Otis et al. 1978) but since then they have undergone considerable development (Nichols 1992). Estimators under this branch of method can be used to model 1) capture probabilities being heterogeneous among individual animals in a population as a result of gender and age, 2) behavioural response to trapping or 3) temporal variation in capture probabilities.

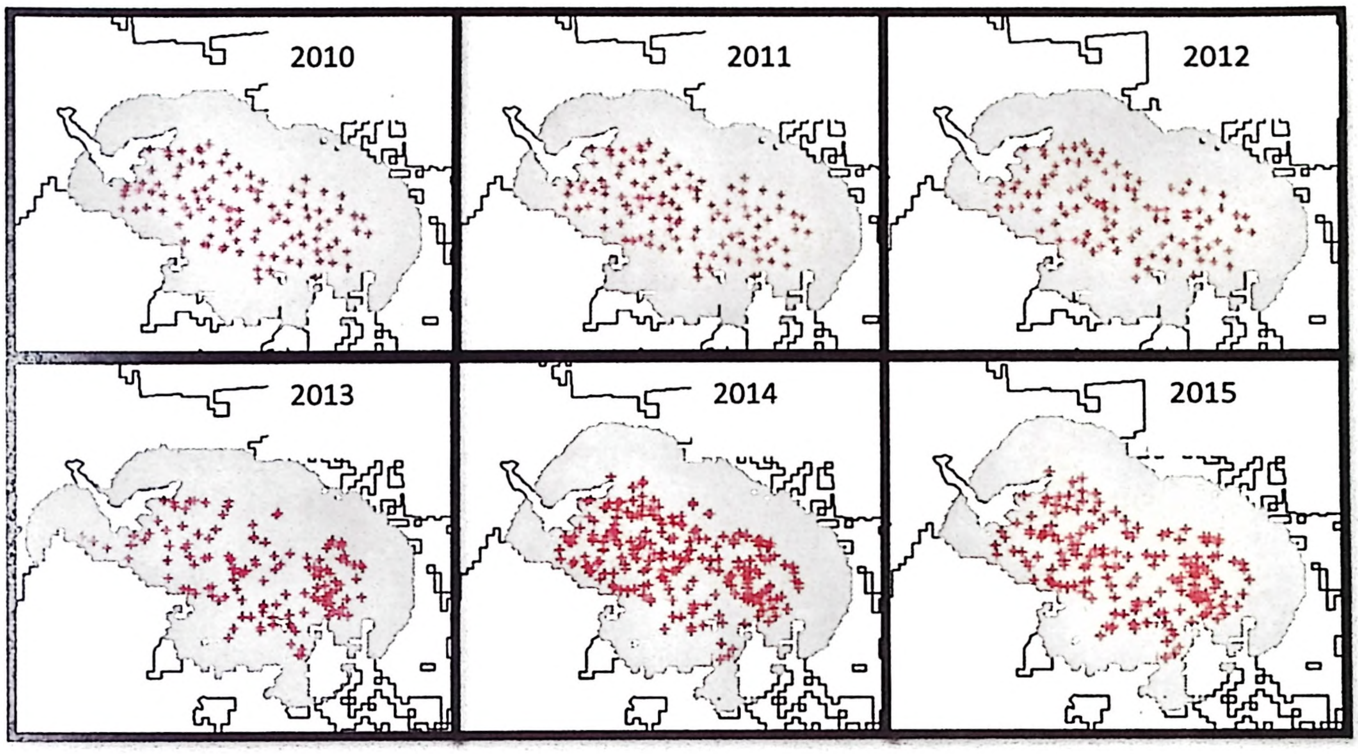
In this chapter I use camera trap based CMR across my current research a constant area of 500 km^{2}from 2010-2015 in Corbett National Park to estimate 1) abundance 2) density of tigers and using these estimates 3) estimated growth rate and trend in tiger population.

3.2 Methods

3.2.1 Field Methods

I used capture-mark-recapture (CMR) in a robust design framework (Pollock 1982) by camera trapping 521 km^2 area of Corbett National Park consistently between 2010-2015. Camera trap units that function on activity and passive infrared triggering mechanism were deployed to photograph tigers. Camera traps were deployed in pairs at each station, on either side of trails, so as to photo-capture both flanks simultaneously of each passing animal. We deployed our camera traps in a protective iron cage to avoid/ minimize damage by elephants. Distance between camera trap stations was maintained between 1 to 1.5 km so as to ensure no "holes" in the sampled area. This high camera density of 1-2 cameras per 5 km^2 (Fig. 3.1) ensured that all tigers in the study area had a good chance of photo-capture with no tiger having zero probability of photo-capture (Amstrup *et al.* 2010).

Figure 3. 1: Map showing Camera traps locations (+) with a buffer of 8 km (as suggested by "suggest.buffer" in package secr)overlaid as tiger habitat mask and model space for spatially explicit capture-mark-recapture for the years 2010-2015 in Corbett National Park.



Camera trap stations were selected based on reconnaissance sign surveys as well as expert knowledge of local field assistants. Potential camera trap point locations were recorded on the ground using a handheld GPS (Etrex 30 and Garmin 72), these locations were then plotted on Google Earth to select points for camera deployment to adhere to above mentioned camera distance and correct for any sampling holes.

Due to logistic constraints (limited number of camera traps) during the initial years (2010-2012) the study area was sampled in two blocks of ~250km^2 area each. These two blocks were sampled 120-150 days apart. With increased availability of camera traps and trained field staff the entire study area (521 km^2) was camera trapped simultaneously in 2013-2015 (Table 3.1).

Table 3. 1: Details of year-wise camera trap deployment in 521 km^2 area at Corbett National Park, 2010-2015

Year	**Blocks**	**Dates Sampled**	**Camera trap days**	**No. of Camera trap locations**	**Trap nights**
2010	1	May-June	42	58	2436
	2	December-Jan	42	45	1890
2011	1	April-June	42	60	2520
	2	December-Jan	42	45	1890
2012	1	April-June	42	60	2520
	2	December-Jan	42	45	1890
2013	-	March-May	42	150	6300
2014	-	March-June	42	222	9324
2015	-	March-May	42	167	7014

3.2.3 Analytical Methods

Photographic captures and subsequent identification of tiger individuals through program EXTRACTCOMPARE (Hiby *et al.* 2009) yielded capture histories of individuals in the standard X-matrix format (Otis *et al.* 1978). All CMR analyses excluded cubs (< 1 year old) because of their low photo-capture probability and high mortality (Karanth *et al.* 2006). Remaining tigers were grouped into a single age class because of difficulty in differentiating between adults and sub-adults from camera trap photos (Sadhu *et al.* 2017).

Each of year of our sampling consisted of 42 camera trap nights, between 2010-2012 sampling was carried out in two blocks (see Appendix, Table S.1). By merging the blocks for analysis we could likely violate the population closure assumption required for abundance estimation. Tigers are long lived in comparison to our sampling interval (Mazak, 1981). We therefore tested if model selection and abundance estimates differed when (a) the two blocks were analysed separately (see Appendix, Table S.1, S.2) and (b) data from the two blocks were merged for a single analysis (see Appendix, Table S.3-S.6). Total population abundance for each year for this block analysis was estimated using a more parsimonious model (see Appendix, Table S.3) in MARK that did not account for sex based heterogeneity in detection and considered transition parameters to be constant. This approach was preferred for estimating total population size as a simpler model provided better precision on total abundance estimates. Since results from separate analyses of the two blocks and the combined analysis yielded abundance estimates that were not different from each other (see Appendix, Table S.6-S.7), we subsequently report results from the combined dataset analyses as this increased sample size allowed us to estimate gender specific parameters.

3.2.3.1 Abundance, Spatially Explicit Density and Population trend

Abundance ($\widehat{N}$) was estimated using closed capture - mark- recapture framework in program MARK 8.x (White and Burnham 1999). We modelled individual detection probability (capture probability (p) and recapture probability (c)) by addressing the following sources of variability:

1) We hypothesised that detection of tigers was likely to differ between sexes since territory size and movement rates differ between males and female tigers (Sunquist 1981, Smith 1993) and as also observed in jaguars (Sollman *et al.* 2011). We modelled this potential source of

variability in capture probabilities by incorporating sex as a covariate in the detection model.

2) Camera trap density was relatively low at 1 per 5 km^2 for the years 2010-2012 compared to a relatively high camera trap density of 2 per 5 km^2 for 2013-2015. We expect that detection probability of tigers would be higher during years (2013-2015) with higher camera trap density. We therefore, modelled detection with two-time period effects; period 1) 2010-2012 with low camera trap density and period 2) 2013-2015 with high camera trap density.

The full detection model (P) was ($P \sim p_{(m(ct),\ f(ct),\ u(ct))};\ c_{(m(ct),\ f(ct),\ u(ct))}$) where capture (p) and recapture (c) were different for male (m) , female (f) and unsexed tigers (u) for the two time periods (ct) that differed in camera density.

By accounting for heterogeneity caused by gender, effect of camera trap density along with traditional behaviour response ($p \neq c$) (Otis *et al.* 1978, Williams *et al.* 2002) we address the specific conditions in our study that could potentially account for variation in detection probability of tigers.

Density ($\widehat{D}$) was estimated through likelihood based spatially explicit capture recapture of tigers (Efford 2004, Borchers and Efford 2008) using package *secr ver.* 3.0.1 (Efford 2017) in program R *ver* 3.4.1(R Core Team 2013). We used function "suggest.buffer"to decide the buffer around the camera trap array. The mesh size was 500 *500m, which is one third of the sigma of tiger (appropriate size as suggested by

Efford 2018). Non forest and water was considered as non habitat while making the mask for the analysis.

Detection corrected number of males and females were estimated from our best model in MARK to arrive at sex ratio.

Another important parameter for population dynamics is the population trend. We regressed natural log of tiger density against years (2010 to 2015). The slope of the regression provides an estimate of the instantaneous growth rate (r) (Caughley 1977, Skalski 2005). A significant positive slope implies an increasing population and a negative slope implies population decline, while a slope of zero implies a stationary population (Caughley 1977). For a population near its carrying capacity we expect the growth rate to not be significantly different from zero. However, for a species like tiger with high intrinsic i reproductive potential (Mazak 1981), we expect substantial recruitment rate that sources individual to the larger landscape through dispersal.

3.3 Results

A total sampling effort of 35,784 camera-trap-nights yielded 6202 photographic captures of 307 individual tigers during our six-year study (2010-2015) (Table 3.2). Of the 307 individuals, 130 were females, 118 males and 59 individuals whose gender could not be ascertained. Individuals in the unidentified gender group had 1-2 captures in a given year and were not photo-captured in succeeding years.

Table 3. 2: Details of sampling effort, detections and number of individual tigers photo-captured at Corbett National Park, 2010–2015

Primary Period	CT density	Trap-nights	#photo-captures	M_{t+1}	Cumulative no. of tigers	#males	#females	#breeding females
2010	Low	4326	466	89	89	36	43	11

2011	High	4410	461	98	129	34	37	10
2012		4410	925	93	162	30	33	8
2013		6300	1183	109	201	31	39	8
2014		9324	1135	118	251	34	62	7
2015		7014	2032	110	307	50	62	16

CT density- Camera trap density; M_{t+1}- unique individuals photo-captured

3.3.1 Abundance, Density and Recruitment

Tiger detection probability was best explained by the model that accounted for (a) gender based differences (b) behavioural response of tigers to camera traps and (c) the camera density (Table 3.3). The closest competing model differed by a Delta AICc of 3.71 (Table 3.3).

Table 3. 3: Model selection statistics for detection models using capture mark recapture on tiger photo-capture data from Corbett National Park, 2010–2015

Sno	**Model**	**AICc**	**Delta AICc**	**AICc Weights**	**Model Likelihood**	**Num. Par**	**Deviance**
1	$p_{(M(ct), F(ct), U(.))}c_{(M(ct), F(ct), U(.))}$	17408.82	0.00	0.82	1.00	14	17217.96
2	$p_{(g.ct)}c_{(g.ct)}$	17412.53	3.71	0.13	0.16	16	17217.63
3	$p_{(g)}c_{(g)}$	17521.81	112.98	0.00	0.00	9	17341.03
4	$p_{(ct)}c_{(ct)}$	17743.04	334.22	0.00	0.00	7	17566.29
5	$p_{(.)}c_{(.)}$	17898.81	489.99	0.00	0.00	5	17726.07
6	$p=c_{(g)}$	17917.80	508.98	0.00	0.00	6	17743.06
7	$p=c_{(t)}$	18148.45	739.63	0.00	0.00	5	17975.72
8	$p=c_{(.)}$	18306.76	897.94	0.00	0.00	4	18136.03

p- capture probability; c- recapture probability; g- gender; M-Males; F-Females; U- Unidentified gender; ct- are the two time periods differing in camera trap density.

Detection probability increased with increase in camera trap density (Table 3.4), more so in females (from 0.05 to 0.07) as compared to males.

Table 3. 4: Capture (p) and recapture (c) probability of females, males and unidentifiable gender for high and low camera trap density years, Corbett National Park, 2010-2015)

Gender	**Camera trap density**	**Detection parameters**	**Estimate (SE)**
Female (n=130)	**Low**	p	0.05 (0.007)
		c	0.12 (0.005)
	High	p	0.07 (0.007)
		c	0.18 (0.005)
Male(n=118)	**Low**	p	0.06 (0.007)
		c	0.14 (0.006)
	High	p	0.06 (0.007)
		c	0.20 (0.007)
Unid (n=59)	**Low and High**	p	0.002 (0.002)
		c	0.02(0.004)

Tiger numbers ranged from 109 to 139 over the 6 years of study (Table 3.5). Overall σ, the movement parameter was larger for males (2.1 ± 0.24 km) compared to females (1.1 ± 0.75 km). Capture and recapture probability for males and females was different. Tiger density was stable at 14 ± 3 per 100 km^2 from 2010-2015 (Table3.5). Detection corrected sex ratio was 0.80 ± 0.13 male/female from 2010 to 2015 (Table 3.5).

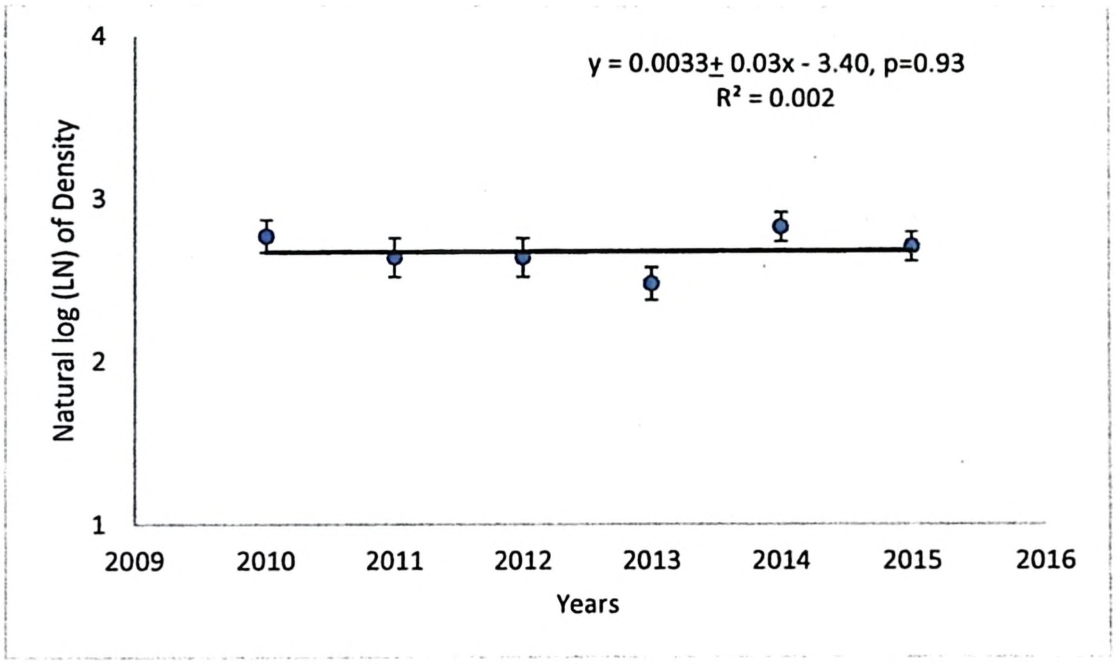
3.3.2 Population trend:

The slope (r) of the regression of ln (D) versus years was not different from zero ($r=0.003\pm0.03$, $p=0.93$, $R^2=0.002$) suggestive of a stationary tiger population (Fig.3.2).

Table 3. 5: Gender specific abundance ($N_t(M)$, $N_t(F)$, $N_t(U)$), overall Population estimate (N_t), detection corrected Male to Female ratio (M:F), spatially explicit density($\widehat{D}$) (per 100 km^2) along with associated statistics of detection probability (go) and movement parameter (σ) (in Km), in Corbett National Park between 2010-2015

	Abundance estimates		**Gender-wise Abundance estimates from MARK**				**Density estimates from SECR**				
Year	N_t - MARK (SE)	N_t - SECR(SE)	N_t F (SE)	N_t M (SE)	N_t U (SE)	M:F	$\widehat{D}$ (SE)	σ F (SE)	σ M (SE)	g_0 F (SE)	g_0 M (SE)
2010	124 (8.92)	119 (4.91)	50(4.10)	43(3.39)	62(90)	0.84	16(1.6)	1.43 (0.06)	2.12 (0.09)	0.03 (0)	0.03(0.003)
2011	117(8.57)	120 (7.43)	43(3.67)	40 (3.37)	85(123)	0.92	14(1.6)	1.06 (0.03)	2.01 (0.08)	0.12 (0.01)	0.05(0.004)
2012	109(8.15)	102 (5.22)	39(3.38)	36(3.01)	91(129)	0.91	14(1.6)	0.8(0.02)	2(0.05)	0.05 (0)	0.2(0.002)
2013	109(8.15)	103 (2.9)	46(3.81)	37(3.08)	45(70)	0.79	12(1.2)	1.3(0.05)	2.56 (0.1)	0.01 (0)	0.08(0.009)
2014	124(6.25)	121 (4.5)	68(3.22)	37(2.36)	51(75)	0.55	17(1.5)	1.04 (0.7)	1.8(0.6)	0.3(0.02)	0.09(0.006)
2015	139(6.74)	139 (3.22)	68(3.22)	56(3.03)	22(39)	0.81	15(1.4)	1(0.07)	2.18 (0.02)	0.2(0)	0.04(0.003)

Figure 3. 2: Natural log of tiger density with standard error plotted against years for 2010-2014 in Corbett National park



3.4 Discussion

Industrial development, mining, palm plantations, highways and other linear structures are fragmenting prime wildlife habitat across Asia. Large carnivore conservation is limited by shrinking space as forested areas are converted into smaller islands. This problem is amplified in India which is a hub for development but is yet home to 70% of the world's wild tiger population. Tiger occupancy within India's tiger landscapes is maintained by protecting at least one significant source population within each landscape. Through the first long-term study on tigers in Corbett National Park we assess the status of one such important population in the Indian Terai. Estimated tiger density (14 ± 3 per 100 km^2) within Corbett National Park is one of the highest recorded in the world. This when compared with

Contractor 2007, is lower (19 ± 1.6 per 100 km^2) since in this study the density was estimated using non-spatial CMR method. When we reanalyzed the results to estimate non-spatial density from our data, we found that it was similar (18 ± 1.2 per 100 km^2 to the one reported by Contractor in for 2006-07. This shows that tiger population has been constant since 2010. The study investigates how large carnivore populations might behave when crowded to this extent.

By pooling data from both blocks our estimates of abundance were not affected (see Appendix, Table S.7). Since both adjacent blocks had high tiger density, movement between them was restricted and only 4-5 individual tigers were common between the two adjacent blocks (amounting to 4% of the population). Therefore, the issues of the block design are restricted to a negligible proportion of population and is unlikely to alter our inferences.

Larger movement of males, *i.e* larger home range leads to a greater sigma in SECR compared to females. Camera trap study on Jaguars in central Brazil reported male capture probability (0.49± 0.05) to be five times more than the females (0.09± 0.04, Sollman et al 2011, Harmsen et al 2017). Comparing detection and movement parameters across different long-term camera trapping studies on tigers, we found that tigers in Corbett had a higher detection probability at the home range center than the rest, while CNP tigers had the smallest sigma (an estimate of home range radius) (Table 3.6). Implying that tigers had smaller home-range in Corbett and used their area much more intensively.

Table 3. 6: Comparative review of camera trap based spatially explicit capture recapture studied carried out on tigers from across their range

Study	**Site**	$\hat{D}$ **(SE)**	**σ F (SE)**	**σ M (SE)**	**g_0 F (SE)**	**g_0 M (SE)**	**M:F**
Sadhu et al. 2017	Ranthambhore	6.8 (0.8)	1.6 (0.16)	2.48 (0.51)	0.06 (0.01)	0.05 (0.01)	0.76
Kumar et al. 2019	Kanha	4.98 (0.2)	1.99 (0.25)	2.75 (0.05)	0.04 (0.0)	0.03 (0.0)	0.66
Chanchani 2016	Dudhwa	1.99(0.06)	2.55(0.25)	4.57 (0.4)	0.04 (0.0)	0.04 (0.0)	0.53
Chanchani 2016	Katarniaghat	2.21 (0.66)	2.61 (0.35)	5.09 (2.82)	0.05 (0.01)	0.05 (0.01)	0.47
Chanchani 2016	Kishenpur	5.21 (0.24)	1.96 (0.12)	3.04 (0.96)	0.07 (0.01)	0.07 (0.01)	0.35
Bisht et al. 2019	Corbett	14 (3)	1.1 (0.1)	2.11 (0.11)	0.12 (0.05)	0.08 (0.03)	0.8

$\hat{D}$- spatially explicit density per 100 km^2; σ - movement parameter (in km) ;go- detection probability ; M:F :detection corrected Male to Female ratio

Tigers in our study had high capture probabilities (males 0.96,SE 0.09; females 0.89, SE 0.02) and increase in camera trap density resulted in increased capture probability by 12%, mainly due to better detection of the proportion of the population that inherently had low detectability (unsexed tigers). While for sexed individuals (males and females) the capture probability increased by about 4%. Tiger population in Nagarhole and Russian Far East were observed to increase at 3-6% (Karanth et al. 2004 and Miquelle 1999), while in Suklaphanta in Nepal the population showed 21% increase (Thapa et al. 2017). With a growth rate no different than zero in the current study the population seems to have reached its carrying capacity and as mentioned earlier that tiger density has remained constant since 2006-07.

CHAPTER 4: VITAL RATES OF TIGERS IN CORBETT TIGER RESERVE

4.1 Introduction

Prioritising conservation efforts for source populations of tigers is seen as a solution to limited funds and manpower, since these source populations are found in 6% land area (Walston *et al.* 2010). Knowledge of the demographic parameters and population dynamics of such high density populations can help tiger recovery by guiding conservation management actions within source habitats and the larger landscapes. The best approach to studying wildlife demography is through telemetry, however such studies are constrained by the number of animals that can be radio-tagged due to limitation of resources and permission for capture. Alternatively, camera trap based open capture-mark-recapture (CMR) has proved to be a useful approach to study vital rates of large carnivore populations (Karnath *et al.* 2006, Sharma *et al.* 2014, Duangchantrasiri *et al.* 2016, Majumdar *et al.* 2017, Harmsen *et al.* 2017).

The earliest and some of the most general open CMR models were developed by Cormack (1964) and extended by Jolly (1965) and Seber (1965). These models required equal catchability and survival rates of animals at each sampling time. They enabled one to estimate population sizes, survival rates and birth numbers for all the samples, Pradel (1996) and Schwarz and Arnason (1996) integrated recruitment in the likelihood of these models. Concerns over equal catchability and survival rates led to development of robust open CMR models (Pollock 1982). This method integrated different sampling methods (closed CMR and open CMR) to allow for unequal catchability and separate recruitment from immigration and to estimate temporary emigration (Pollock 1982). Recent approach using spatially explicit open capture (SECR) CMR models have attempted to distinguish between emigration and mortality (Ergon & Gardner 2014, Gardner et al., 2018). However, these approaches are still under development (Efford 2019) and require a very large scale camera trapping to capture dispersal events of large carnivores, making them impractical for application (Ergon & Gardner 2014).

Though camera trap based open CMR approach addresses the limited sample size of telemetry studies, the vital rates obtained by open CMR cannot distinguish between mortality and permanent emigration (Pollock 1982). However, information generated by CMR is useful in understanding many aspects of demography that include vital rates such as apparent survival, recruitment, movement, time specific detection corrected sex ratio and percentage of breeding females in the population.

Long-term work on tigers in the Nepal *Terai* has provided information on tiger demography through telemetry (Sunquist 1981, Smith 1993) and camera trapping (Barlow *et al.* 2009). Most of our knowledge on population dynamics and vital rates of tigers in India is from central India (Schaller 1967, Panwar 1979, Majumdar *et al.* 2017, Sadhu *et al.* 2017) and from the Western-Ghats (Karanth *et al.* 2006). While Corbett on the Indian side of *Terai* harbours the single largest tiger population in a single protected area in the world, estimated at 169-261 tigers, with a density of 16± 1.60 tigers per 100 km^{2} (Contractor 2007, Bisht *et al.* 2014), this population remains data deficient in our understanding of tiger demography and ecology.

Under this objective I aim to understand the demographic processes that operate in high density tiger populations like Corbett. Corbett provides a unique opportunity to study a system that has been able to sustain one of the highest tiger densities in the world. The mechanisms behind this are of importance in current times of limited space and vanishing large mammals. The demographic parameters estimates from a high density tiger population at/or approaching carrying capacity can be used for model-based predictions (Karanth and Stith 1999) so as to gain an understanding of long term population dynamics as well as form a basis for management interventions. Mechanisms behind sustained high density of tigers in Corbett spells hope for tiger conservation efforts. It shows that establishing source tiger populations similar to that of Corbett within each tiger landscape, is the first step towards global tiger recovery. This information will also help set realistic targets for achievable tiger numbers, enabling work towards reaching the set objective of "TX2 commitment" by Tiger range countries (https://www.wwf.de/fileadmin/fm-wwf/Publikationen-PDF/Global-Tiger-Recovery-Program-Nov-4.pdf, Global Tiger Initiative, Global tiger recovery program 2010-2022).

4.2 Methods

4.2.1 Field Methods

I used capture-mark-recapture (CMR) in a robust design framework (Pollock 1982) by camera trapping 521 km^2 area of Corbett National Park consistently between 2010 - 2015. The field methods were same as mentioned in chapter 3, section 3.2.1.

4.2.2 Analytical Method

Photographic captures and subsequent identification of tiger individuals through program EXTRACTCOMPARE (Hiby *et al.* 2009) yielded capture histories of individuals in the standard X-matrix format (Otis *et al.* 1978). All CMR analyses excluded cubs (< 1 year old) because of their low photo-capture probability and high mortality (Karanth *et al.* 2006). We grouped remaining tigers into a single age class because of difficulty in differentiating between adults and sub-adults from camera trap photos alone (Sadhu *et al.* 2017). Owing to a large sample size (n=307) and ability to sex most individuals we were able to obtain gender specific parameter estimates.

We analysed capture data under the Robust design initially proposed by Pollock (1982) and subsequently modified by Kendall *et al.* (1995 and 1997). All analysis were done in program MARK 8.x version 2017 (White and Burnham 1999). Our study consisted of six (2010-2015) years of data with each year as a "primary period" (Pollock 1982, Kendall *et al.* 1995, 1997, Williams *et al.* 2002). The tiger population was expected to be open to gains and losses between these primary periods while closed within the duration of sampling (42 days secondary periods) within each year. Pollock's (1982) robust design was a two-stage analysis where abundance was estimated using closed-population models for each primary period, while transition parameters were estimated between primary periods. Kendall et al. (1995, 1997) developed a full likelihood approach that combined Pollock's (1982) two step analysis into a single analysis. The full likelihood approach allows an animal to be unavailable for capture at any given time (or a temporary emigrant). The probability of availability is modelled to be (a) completely random or depends on whether the animal was (b) available for capture in the previous primary period or (c) actually captured in the previous primary period (Kendall *et al.* 1997). We first modelled capture probability (*detection models*) and subsequently, conditioning on the best selected detection model, we modelled state and transition parameters of interest (*i.e.* abundance, survival and movement) that were in consonance with tiger ecology.

Each of our primary period consisted of 42 camera trap nights (secondary periods). Between 2010-2012 sampling was carried out in two blocks (see Appendix, Table S.1). Between 2012-2013, due to shift from two block sampling to a single block, tigers from the second block were exposed to an interval of six months between primary periods instead of 12 months. For block wise and combined block analysis refer chapter 3 section 3.2.3.

4.2.2.1 Detection models

We modelled individual detection probability (capture probability (p) and recapture probability (c)) by addressing different sources of variability, for details refer chapter 3, section 3.2.3.1.

4.2.2.2 Detection and Transition models

Using the best detection model(s) we subsequently model the detection and transition parameters *viz.* abundance, survival, temporary movements and recruitment. For these parameters we evaluate the following hypotheses:

SURVIVAL

There was no reason to suggest that in CTR habitat, prey or poaching differed between study years that could affect survival rates. Hence, we did not expect survival rates to differ between years. However, males and females have differential life history traits (Smith 1981), and should have different survival probabilities. We expected males to have lower survival compared to females as observed in most mammalian species (Krebs 1972). We therefore modelled survival as constant (null model $S_{(.)}$) or differing between sexes ($S_{(g)}$).

MOVEMENT

We did not expect movement parameters to change between years for the same reason as mentioned above. Males are the dispersing sex in tigers while females are more philopatric (Smith 1993, Sunquist 1981), we therefore expected movement in and out of home range the study area to differ between sexes. Corbett has one of the highest tiger densities in the world (Contractor 2006, Bisht *et al.* 2014) and therefore competition for resources (food and mates) would also likely be high. If we found movement estimates to be very small (e.g <1%) for either gender we considered them to be negligible and in our subsequent analysis we fixed them at zero for parsimony and ease of computation.

Two movement parameters (Kendall et al. 1997) i.e. temporary emigration (G”) and temporary immigration (1-G’) as defined below, were modelled.

(a) Temporary Emigration (G’’) is the probability of going out of study area in a primary period if the animal was present in the previous primary period but remaining within the super population and;

(b) Probability of staying away (G’) from the study area in a primary period given that the animal was part of the super-population in the previous primary period.

We fitted 16 models for the entire robust design analysis. We used sample size corrected Akiake’s information criteria (AIC_c) (Akiake 2011) to select models which best explained our data from candidate competing models. To account for uncertainty associated with model selection we used model averaging by AIC_c weights to average model parameters (Akaike 2011).

4.2.2.3 Recruitment

Recruitment is the number of new individuals added to the population in time t per individual at time $t - 1$. Recruitment in case of a camera trap study is the product of fecundity and survival from cub to >1-year-old tigers as well as immigrants from neighbouring areas. We estimated number of recruits (B_t) in time t as;

$$B_t = \hat{N}_{t+1} - \hat{N}_t \times S$$

where $\hat{N}_{t+1}$ = abundance estimate at time $t + 1$, $\hat{N}_t$ = abundance estimate at time t, S = survival probability (Skalski, Kristin, & Millspaugh, 2010).

4.2.2.4 Reproductive Potential

We examined each photo capture event of females and termed them as 'breeding' if they were pregnant or lactating (Sadhu et al., 2017). Full udders and prominent nipples in a breeding female are visible about 7-10 days before parturition and till the cubs are weaned by 165 days (Gittleman, 1986, Smith & McDougal, 1991). From our long-term ad-libitum observations in the study area we found that one of the female's lactation period lasted for 155 days, which was similar to the lactation period mentioned in Gittleman (1986) and Smith & McDougal (1991). We sampled the study area for 42 days in a year, therefore all females that delivered cubs <5 months before our sampling period would comprise the pool of breeding females available for sampling each year.

We estimated the actual number of breeding females (B_f) during the primary sampling by correcting the number of breeding females photo-captured by the detection probability of breeding females. $B_f = n_L/p_{bf.}$ where: n_L= number of breeding females detected in each primary sampling period,$p_{bf.}$=probability of detecting a breeding female.

Since birth seasonality is not profound in tigers (Sunquist, 1981), we consider tigers to breed throughout the year for our computation. Breeding females (B_{fy}) in a year would be:

$$B_{fy} = B_f \times (Days\ in\ a\ Year \div Sampling\ Days) \times (Days\ Detected\ as\ Breeding \div Sampling\ Days)$$

$$B_{fy} = B_f \times (365 \div 42) \times (165 \div 42)$$

Since we could potentially have 8.69 intervals of 42-day sampling in a year and pregnancy/lactation was detectable for 165 days, a single breeding female could potentially be detected in 3.93 sampling intervals in one year.

4.3 Results

4.3.1 Open CMR Robust design based vital rates of tigers

Tiger detection probability was best explained by the model that accounted for (a) gender based differences (b) behavioural response of tigers to camera traps and (c) the camera density. The closest competing model that lacked the variable of two time periods differed by a Delta AIC$_c$ of 3.8 (Table 4.1).

Table 4. 1: Model selection statistics for detection and transition models using the robust design analysis on tiger photo-capture data from Corbett National Park, 2010–2015

	Sno	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
Detection models	1	$S_{(.)}G'_{(.)}G''_{(.)}\,p_{(M(ct),\,F(ct),\,U(.))}c_{(M(ct),\,F(ct),\,U(.))}$	17408.82	0.00	0.82	1.00	14	17217.96
	2	$S_{(.)}G'_{(.)}G''_{(.)}p_{(g,ct)}c_{(g,ct)}$	17412.53	3.71	0.13	0.16	16	17217.63
	3	$S_{(.)}G'_{(.)}G''_{(.)}p_{(g)}c_{(g)}$	17521.81	112.98	0.00	0.00	9	17341.03
	4	$S_{(.)}G'_{(.)}G''_{(.)}p_{(ct)}c_{(ct)}$	17743.04	334.22	0.00	0.00	7	17566.29
	5	$S_{(.)}G'_{(.)}G''_{(.)}p_{(.)}c_{(.)}$	17898.81	489.99	0.00	0.00	5	17726.07
	6	$S_{(.)}G'_{(.)}G''_{(.)}p{=}c_{(g)}$	17917.80	508.98	0.00	0.00	6	17743.06
	7	$S_{(.)}G'_{(.)}G''_{(.)}p{=}c_{(t)}$	18148.45	739.63	0.00	0.00	5	17975.72
	8	$S_{(.)}G'_{(.)}G''_{(.)}p{=}c_{(.)}$	18306.76	897.94	0.00	0.00	4	18136.03
Transition models	1	$S_{(g)}G'_{(F,M=U=0)}G''_{(F,M=U=0)}p_{(M(ct),\,F(ct),\,U(.))}c_{(M(ct),\,F(ct),\,U(.))}$	17404.70	0.00	0.60	1.00	17	17207.77
	2	$S_{(g)}G'_{(.)}G''_{(.)}\,p_{(M(ct),\,F(ct),\,U(.))}c_{(M(ct),\,F(ct),\,U(.))}$	17407.34	2.64	0.16	0.27	17	17210.41
	3	$S_{(g)}G'{=}G''_{(.)}\,p_{(M(t),\,F(ct),\,U(.))}c_{(M(ct),\,F(ct),\,U(.))}$	17408.41	3.71	0.09	0.16	16	17213.50
	4	$S_{(.)}G'_{(.)}G''_{(.)}\,p_{(M(ct),\,F(ct),\,U(.))}c_{(M(ct),\,F(ct),\,U(.))}$	17408.82	4.13	0.08	0.13	14	17217.96
	5	$S_{(.)}G'{=}G''_{(.)}\,p_{(M(ct),\,F(ct),\,U(.))}c_{(M(ct),\,F(ct),\,U(.))}$	17410.14	5.44	0.04	0.07	13	17221.30
	6	$S_{(.)}G'{=}G''_{(g)}\,p_{(M(ct),\,F(ct),\,U(.))}c_{(M(ct),\,F(ct),\,U(.))}$	17411.06	6.37	0.02	0.04	14	17220.20
	7	$S_{(g)}G'_{(g)}G''_{(g)}p_{(g,ct)}c_{(g,ct)}$	17414.18	9.48	0.01	0.01	22	17207.11

S- Survival; G''-Temporary emigration; G'- Probability of staying away ; p- capture probability; c- recapture probability; g- gender; M-Males; F-Females; U- Unidentified gender; ct- are the two time periods differing in camera trap density.

Detection probability increased with increase in camera trap density (Table 4.2), more so in females as compared to males.

Using the best detection model the state and transition model that had the lowest AIC_c (Table 4.2) accounted for gender differences in survival, had no temporary movement for males and unidentified gender class while accounting for random temporary movements in females. Model estimates of survival and movement parameters differed between males and females, with females having higher survival and temporary movements (Table 4.2).

Table 4. 2: Model averaged estimates of capture (p),recapture (c) probability, survival (S) and temporary movement (G’’& G’) for female and male tigers in Corbett National Park, 2010-2015

Gender	**Camera trap density**	**Detection parameters**	**Estimate (SE)**	**Survival (SE)**	**Gamma' (SE)**	**Gamma'' (SE)**
Female (n=130)	**Low**	p	0.05 (0.007)	0.79(0.05)	0.58(0.24)	0.22 (0.06)
		c	0.12 (0.005)			
	High	p	0.07 (0.007)			
		c	0.18 (0.005)			
Male(n=118)	**Low**	p	0.06 (0.007)	0.60(0.04)	0	0
		c	0.14 (0.006)			
	High	p	0.06 (0.007)			
		c	0.20 (0.007)			
Unid (n=59)	**Low and High**	p	0.002 (0.002)	0.59 (0.25)	0	0
		c	0.02(0.004)			

4.3.2 Recruitment and Reproductive Potential

We estimated high recruitment percent of 35 ± 8 %. During each sampling period 32-39% of females were found to be breeding and the proportion of females actually breeding was estimated to be 54.7 (SE 5.1) %, amounting to an average of 28 (SE 3.2) females each year within the study area.

4.4. Discussion

In the first ever long-term monitoring of tigers in the Indian *Terai* we attempt to characterise this population and provide useful and novel insights into this important source population. This study constitutes one of the largest camera trap data set obtained for any large carnivore in the world, enabling us to model complex combinations of parameters (Gerber *et al.* 2014) and for the first time estimate gender specific survival and other vital parameters for tigers.

For the Robust design population closure is a prerequisite for abundance estimation within secondary periods, while the population is open between primary periods for estimates of survival and movement parameters. Therefore, the block approach in sampling (2010-2012) could adversely affect population estimates due to violation of population closure assumption within the primary periods but would not have any influence on other parameter estimates like survival which were addressed with appropriate models. However, independent and pooled estimates of abundance of the blocks did not differ (see Table S.7). Therefore, by pooling data from both blocks the estimates of abundance were not affected. Since both adjacent blocks had high tiger density, movement between them was restricted and only 4-5 individual tigers were common between the two adjacent blocks (amounting to 4% of the population). Therefore, the issues of the block design are restricted to a negligible proportion of population and is unlikely to alter the inferences of the study.

The survival estimated in CMR studies is apparent survival which includes death and permanent emigration. Survival probability varied between genders, where apparent annual survival probability of males (0.60) was much lower than that of females

(0.79). Out of 130 females photo-captured during the study period (2010-15) we identified 61 (~50%) to be residents since they were photo captured in 2 or more primary periods compared to 38% males who were residents. Females are philopatric and this is reflected in their survival rates, while low survival rate of males is characteristic of large carnivores, which are exposed to higher risks and are the dispersing gender in tigers (Smith 1993). None of the published studies on population dynamics of tigers from open CMR have estimated gender specific survival because of relatively small datasets (Karanth *et al.* 2006 n=78, Majumdar *et al.* 2017 n=66 and Duangchantrasiri *et al.* 2016 n=90) (Table 4.3).

Table 4. 3: Comparative review of camera trap based open capture-mark-recapture studies carried out on tigers from across their range.

Parameters	**Nagarhole***	**Huai Kha Khaeng$^+$**	**Pench$^\#$**	**Corbett†**
Survival	0.77(SE 0.05)	0.80-0.96	0.66 (SE 0.04)	0.68(SE 0.02)
Temporary Emigration	0.10(SE0.07)	Not Reported	Not Reported	0.2 (SE 0.08)$^\Delta$
Mean Maximum distance moved-Male (km)	3.74 (SE 0.56)	4.37(SE 1.05)	5.33 (SE 0.91)	4.6 (SE 0.96)
Mean Maximum distance moved-Female (km)	3.74 (SE 0.56)	4.37(SE 1.05)	5.33 (SE 0.91)	2.8(SE 0.77)
Density/100 km^2	9.7(SE 1.8)	1.68 (SE 0.69)	3.70 (SE 0.8)	14 (SE 3.0)

* Karanth and Sunquist 1995, Karanth *et al.* 2006 , Karanth and Sunquist 2000
+ Duangchanstiri *et al.* 2016
# Majumdar *et al.* 2017
† Current study
Δ temporary emigration estimate for the females, males in the study do not show temporary movements

Hence, lack of gender specific estimates from India and across the tiger's range limits comparison of these estimates. The overall estimate of annual survival of adult tigers (0.68) in Corbett was lower than that reported for tigers in South India (0.77, Karanth *et al.* 2006) and in Thailand (0.82, Duangchantrasiri *et al.* 2016). High density likely leads to intense competition which is reflected as depressed survival rates. A telemetry study on Corbett tigers is required to further tease apart emigration from mortality as well as provide insights into dispersal and territoriality.

Corbett tiger population is a paradox of sorts as it maintains a stable high density population yet has low survival rates. With over 54.6 (SE 5.1) % females found breeding each year with a high level of recruitment (35 (SE 8%)) creates intense competition, this likely results in high emigration and turnover rates in the population. This number of breeding females exceeds the number recommended by source populations (20-25 Chapron *et al.* 2008, Gopal *et al.* 2007). Tiger population in Nagarhole and Russian Far East were observed to increase at 3-6% (Karanth *et al.* 2004 and Miquelle 1999). With a zero growth rate in the current study the population seems to have reached its carrying capacity, where recruitment replaces deaths and emigration. Considering the mortality rate of Corbett tigers to be similar to tigers in Ranthambhore which is also at high density (10-16% Sadhu *et al.* 2017), the recruitment in Corbett far exceeded the deaths. This suggests that large number of tigers disperse out of Corbett to maintain a stable density and the turnover is likely caused due to dispersal and births, a major characteristic of a good source population (Pulliam 1988).

CHAPTER 5: TESTING OPENNESS OF A CLOSED POPULATION

5.1 Introduction:

Wide applicability of remotely triggered camera traps in a variety of habitats and ability to provide information on activity pattern, habitat use and reproductive status, has led to an increase in their application in the recent past. This coupled with the rapid progress in the capture-mark-recapture theory (Otis et al. 1978; Pollock et al. 1990) has made camera trap based capture-mark-recapture a very effective tool to estimate abundance and vital rates for a whole range of species with identifiable body marks. This method involves conducting repeated surveys over time and photographing individuals which are uniquely identifiable by their pelage patterns using remotely triggered camera traps. Such surveys yield individual capture histories (X matrices; Otis et al. 1978) which is then used to estimate abundance and other parameters of interest. Camera trap based CMR has been the focal tool used in a lot of monitoring exercises around the world, especially for endangered large carnivores like tigers and jaguars. Hence, success of such research monitoring projects hinges on a robust study design that accommodates all the assumptions of CMR theory.

There are several factors to consider for selecting appropriate study design for a large carnivore abundance estimation. Appropriate scale and adequate spacing between the camera trap stations is important, which is a tradeoff between the logistics and scientific rigour. One of the most important assumptions to be met while estimating population size (N^) under a closed capture estimator is that of population closure, which implies that the population under investigation does not undergo change (birth, death, immigration and emigration) during the period of the study. Population change is inevitable but a good study design should be such that has minimum level (<=5%) of population change. Most of the studies on tigers assume 45 days as relatively short duration for demographic closure, given the longevity of tigers. In CMR studies births and deaths are actually additions and deletions and effect of these are assumed to be minimal for 45 days. However, geographic closure often caused due to the movement of individuals in and out of the sampling grid (i.e., temporary immigration and emigration) for wide ranging animals, can be ensured by having broad spatial coverage. Whether this actually ensures minimal population change or not has not been empirically tested, and we tested this in the current study.

Precision of abundance estimates yielded by the CMR studies are also very important for appropriate monitoring strategies. Without precise (low coefficient of variance) estimates monitoring the success or failure of a research program becomes difficult due to large confidence intervals of the population estimates. Hence sampling issues and optimizing study design to improve precision are of utmost importance. Tigers are typically classified into demographic classes (Karanth and Stith 1999) irrespective of the sexes into: cubs (less than 1-year-old), juveniles (1– 2 years old), breeding adults (3–12 years old), post-dispersal floaters or transients (over 2 years) and evicted breeders (over 12 years). Each gender and demographic class has an associated detection probability with it. Capture probabilities (p^) vary with respect to age (Karanth and Nichols 1998), sex, range size among other factors, it is important to achieve adequate sample sizes (uniquely identified individuals and recapture rates) while estimating population parameters within a capture-recapture framework (White et al. 1982).

In the current study we are trying to find a tradeoff between precise abundance estimates but avoiding population change. Therefore, in this study, we evaluate the influence of number of trap days on the assumption of geographic and demographic closure and their relationship with capture probability (p^) by subsampling capture histories obtained for tigers from 50 trapping stations within the Corbett National Park, Uttarakhand, India. We suggest sampling durations such that studies can optimize their sampling strategies using similar analytical approach to attain desired level of precision within a site.

5.2 Field Methods

We camera trapped an area of ~100 km^2 in Corbett National Park continuously for a year, from May 2012 to June 2013. We deployed camera trap units that function on activity and passive infrared tripping mechanism, to photograph tigers in the area. Camera traps were deployed in pairs at each station on either side of trails so as to photo-capture both flanks simultaneously of each passing animal. Distance between camera trap stations was maintained between 1 to 1.5 km so as to ensure no "holes" in the sampled area. This high camera density (Fig. 5.1) ensured that all tigers in the study area had a good chance of photo-capture with no tiger having zero probability of photo-capture (Amstrup *et al.* 2010). Camera trap stations were selected based on reconnaissance sign surveys as well as expert knowledge of local field assistants. Potential camera trap point locations were recorded on the ground using a handheld GPS (Etrex 30 and Garmin 72), these locations were then plotted on a GIS platform

First, we aim to understand how abundance estimates vary with sampling time, as this relationship provides insights into the 'openness' of a 'closed' population. With this aim, we estimated tiger abundance for increasing sampling windows (15-90 days) in Closed Mark Recapture (CMR) framework. We created X matrices from 50 random start points for each of these sampling windows. We estimated the population size ($\widehat{N}$) and associated variances against each iteration (Otis et al. 1978; White and Burnham 1999) by modeling capture ($\hat{p}$) and recapture ($\hat{c}$) probabilities. This exercise depicted the effect of sampling time on abundance estimation (MLE and variance).

Subsequently, we demonstrated the postulated effect(s) of sampling process and determined the minimum adequate duration to negate these effects (i.e., capture intraspecific difference in detectability, should it exist) for a given trap density. For this, we simulated detection matrices by drawing random samples for k occasions ($k = 5, 6, 7 \ldots 15$) from known parameters: $N = 26$, probability of mixture $pi = 0.6$, capture probability of group 1, $p_1 = 0.15$ and capture probability of group 2, $p_2 = 0.5$ that were estimated from our intensively studied population. The simulated detection matrices were analysed in CMR framework to estimate abundance and compute bias (percentage deviation from the true parameter value) against increasing occasions. Through this exercise, we identified the shortest trapping duration (t_{min} occasions) required to minimize abundance bias resulting from unaccounted intraspecific difference in detectability. This gave us effect of time (sampling window length) on abundance and associated precision if any. Obtaining the minimum number of days required from the above analysis, to capture the heterogeneity in the population we then obtained abundance estimates for varying sampling window. We wanted to see how long should the sampling window be so that the estimated abundance has least bias and high precision. We simulated data (1-0 or X matrix) for the n number of individuals that were photo captured during the study period, using the values of probability of mixture (pi), capture probability ($\hat{p}$) and recapture probability ($\hat{c}$) from the actual population estimates. This simulated data was then used to estimate abundance estimates (similarly as explained earlier) for varying sampling window and compared to the truth (n number of individuals photo captured) to see how precision and bias varies with time.

Using the sampling window which was a trade-off between bias and precision, we set up a Robust open population CMR design experiment (Pollock ,1982, for details refer Chapter 4, section 4.2.2). Here length of each primary period was decided by the previous experiment and days between two primary period varied from 0-75 days. This led to population being progressively open and gave estimates of survival, recruitment and movement along this varying degree of openness.

We analysed this data in MARK for the estimates of survival, recruitment and movement. Under the Robust Design the following parameters were estimated using:

1) Pradel Model: Survival (S) – this is the apparent and Recruitment (f)

   Survival in case of CMR studies is the apparent survival and recruitment is the number of new individuals added to the population in time t per individual at time t-1. Recruitment (f)in case of a camera trap study is the product of fecundity and survival from cub to > 1 year old tigers as well as immigrants from neighbouring areas.

2) Pollock Model: S, Temporary Emigration(G") and Temporary Immigration (G')

Two movement parameters (Kendall *et al.*, 1997) i.e. temporary emigration (G") and temporary immigration (1-G') as defined below, were modelled.

(c) Temporary Emigration (G'') is the probability of going out of study area in a primary period if the animal was present in the previous primary period but remaining within the super population and;

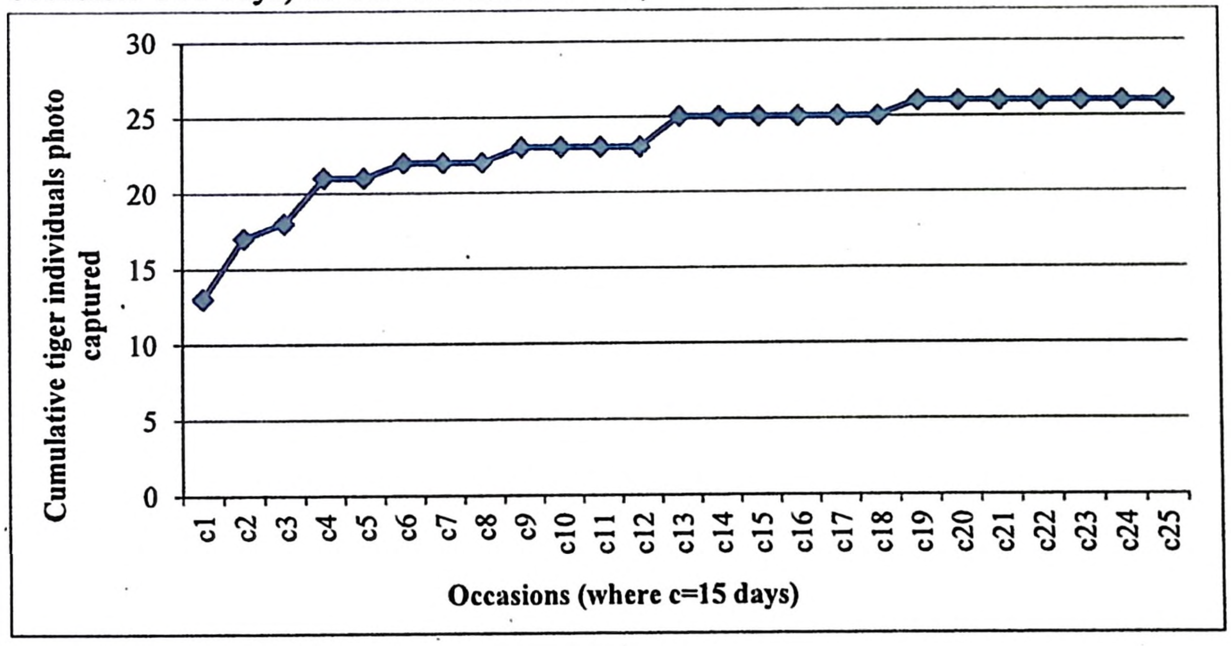
(d) Probability of staying away (G') from the study area in a primary period given that the animal was part of the super-population in the previous primary period.

In both models we first built the detection model (pi, p and c), and then Survival (S) and movement (G'' and G') models. We ran Markovian (S(.) G"(t), G'(t)), Random (S(.)G" =G'(.)) and Null (S(.) G" =G' (0)) model. Under the Random movement model the probability of moving between availability states between primary occasions t and t +1 is independent of the previous state of the system, whereas for Markovian movement, the probability of moving between availability states between primary occasions t and t+1 is conditional on the state of the individual at time t–1 and in the Null movement model there is no emigration and hence movement parameters are set to zero. We used AIC and Likelihood Ratio test were used to select the best model. The aim here was not to get an estimate of these demographic parameters but to test the openness during hitherto thought to be closed population sampling periods. For this we estimated total population change using recruitment and mortality rate from Pollock Robust design.

5.4 Results

We obtained 1940 photographs of 26 tigers in 18,475 trap-days. Of these 26 individuals 16 were females and 10 males. During the study period 6 females were found to be lactating. Since Corbett has a high turnover rate, saturation in photo captures of new individual was reached after almost 180 days (Fig. 5.2).

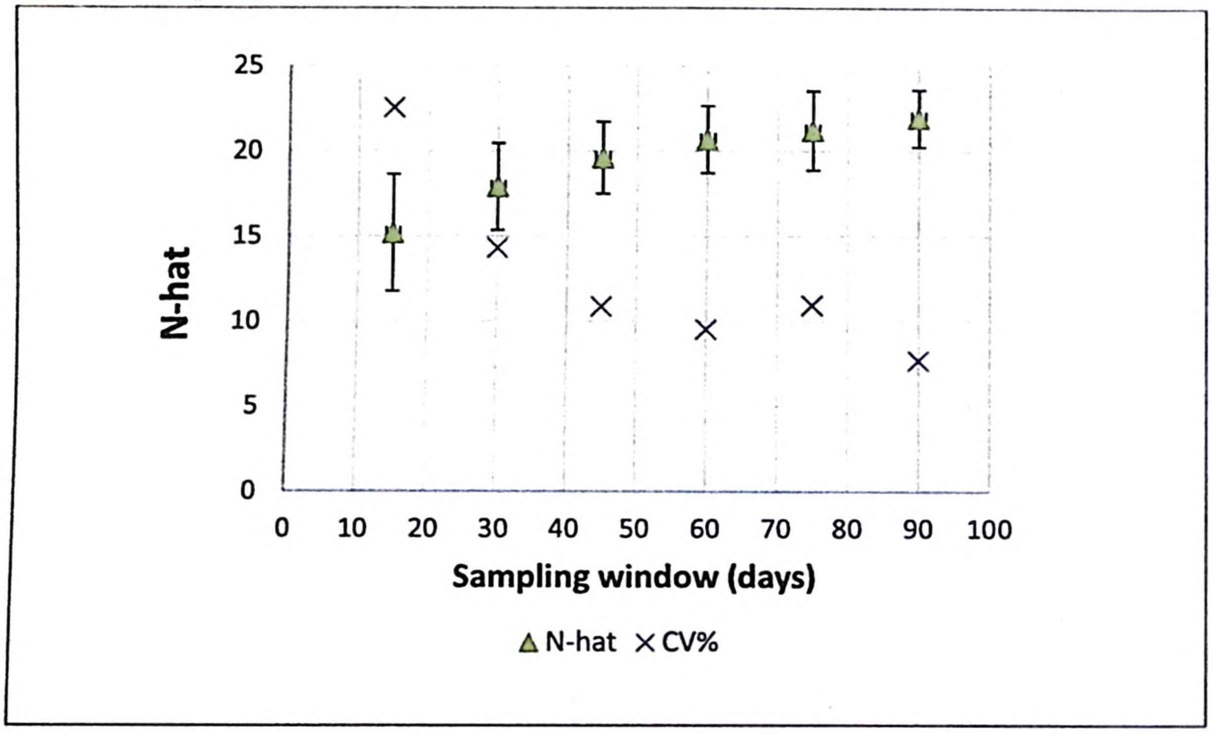
Figure 5.2: Graph showing saturation between photo-captures of new tiger individuals and days (15 days compressed to make one occasion (c1 to c25), 15*25 occasion=375 days) in Corbett National Park,2012-2013



5.4.1 Time-Abundance relationship

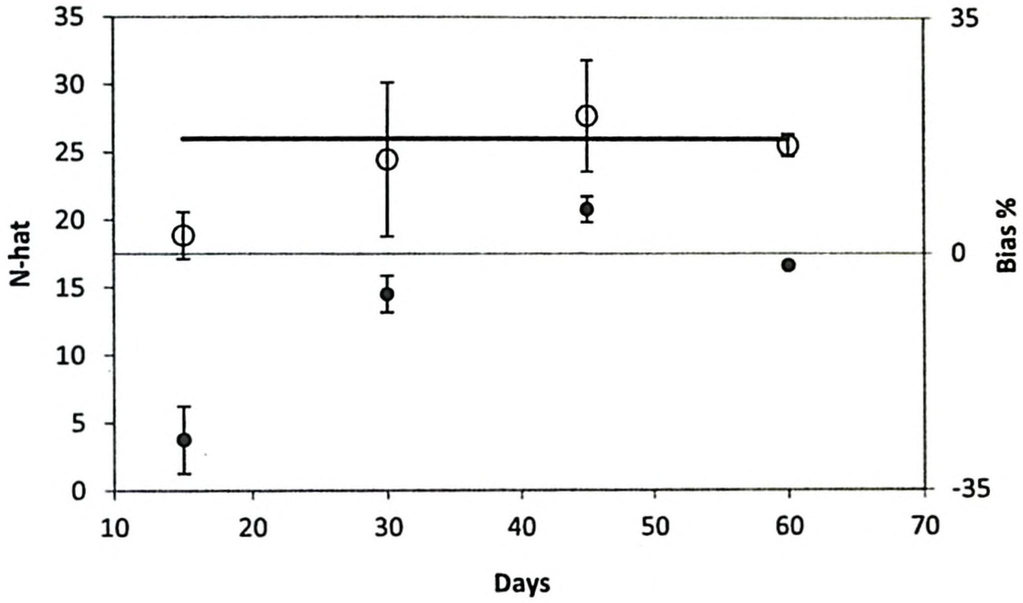
We ran 300 iterations of abundance estimates for 15, 30, 45, 60, 75 and 90 days sampling windows, of these 287 iterations results gave us estimates of abundance. The following graph (Fig. 5.3) shows how with increasing sampling duration abundance increased from 15-22 tigers and precision increased from 22 to 7%.

Figure 5. 3: Graph showing abundance and CV estimates from program MARK, for varying sampling windows in Corbett National Park, 2012-2013



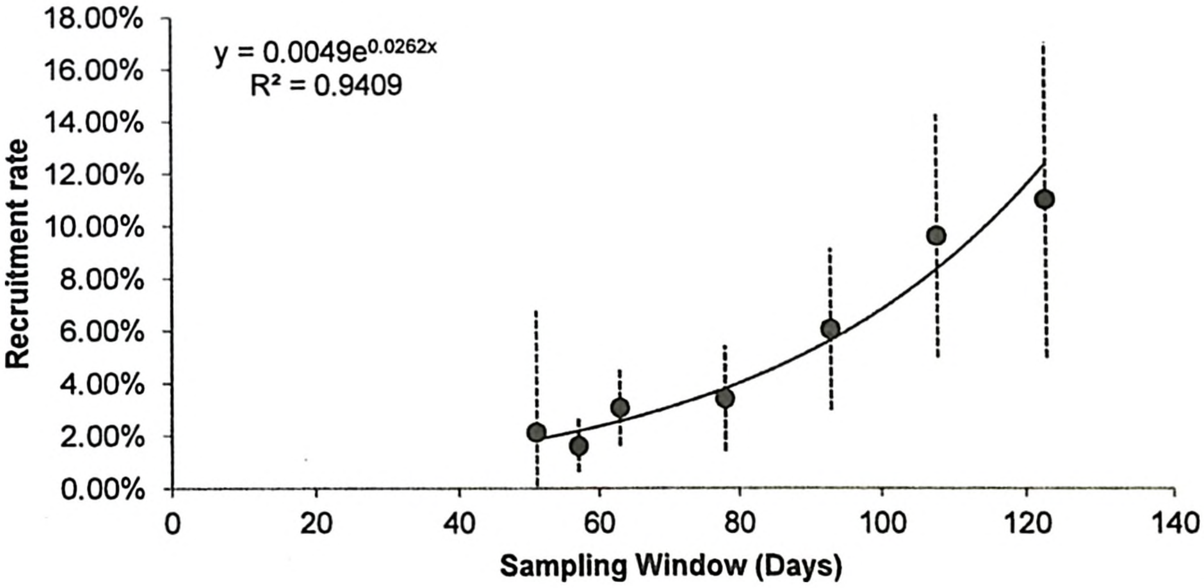
Using 15 days as the minimum number of days required to capture the heterogeneity in the population, we estimated pi, p and c for the population. Using these estimates, the capture history that was produced was then sub-sampled at varying number of days (15-75 days) to estimate abundance. These estimates when compared to the truth (n=26 tigers) (Fig. 5.4) we found that below 20 days the detection probability is over estimated and abundance estimates are underestimated and above this the bias reduces, hence we selected 24 days as the length of the primary period.

Figure 5.4: Graph showing abundance and associated bias estimated from the simulated population plotted against the truth (N= 26, denoted by solid line in the graph), Corbett National Park 2012-2013



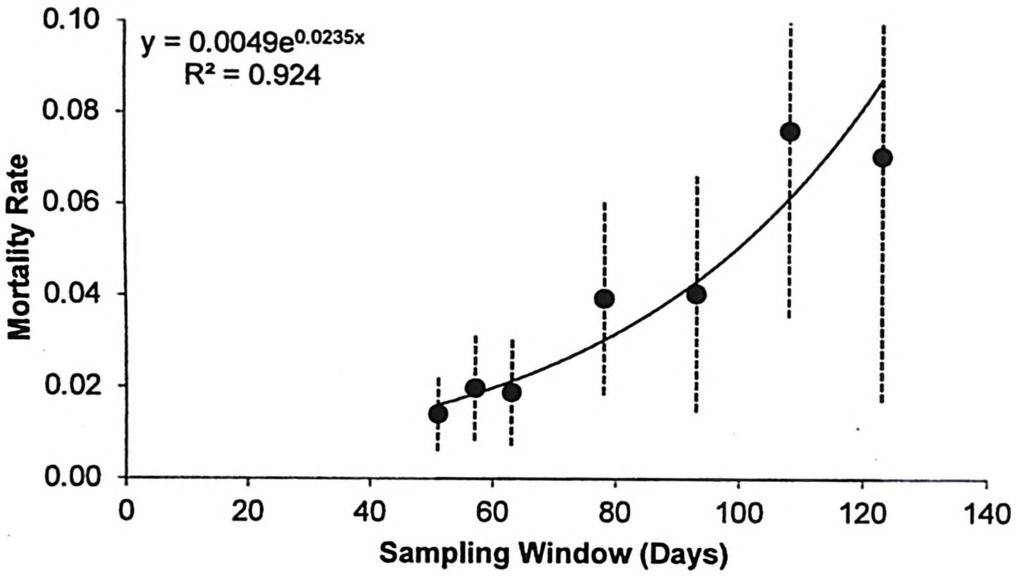
Recruitment rate: Recruitment estimates derived from pradel model ranged from 2 to 12% from 48 to 120 days (Fig. 5.5).

Figure 5. 5: Graph showing recruitment rate against varying sampling days in Corbett National Park 2012-2013



Apparent mortality estimated as 1- apparent survival probabilty, increased from 2 to 8% from 48 to 120 sampling days(Fig.5.6).

Figure 5.6: Graph showing mortality rate (1-S) against varying sampling days in Corbett National Park 2012-2013



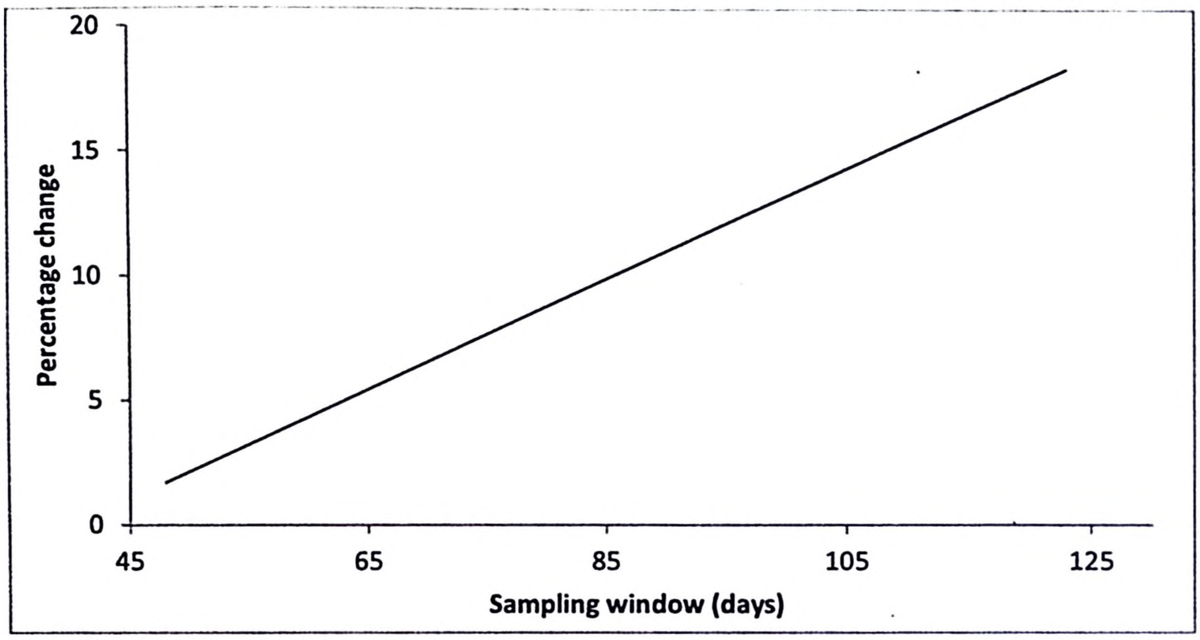
5.4.2 Population Change

Net change in population was more than 5% after nearly 60 days of sampling (Table 5.1, Fig 5.7).

Table 5.1: Percentage of additions, deletions and total population change for each sampling window in Corbett National Park 2012-2013

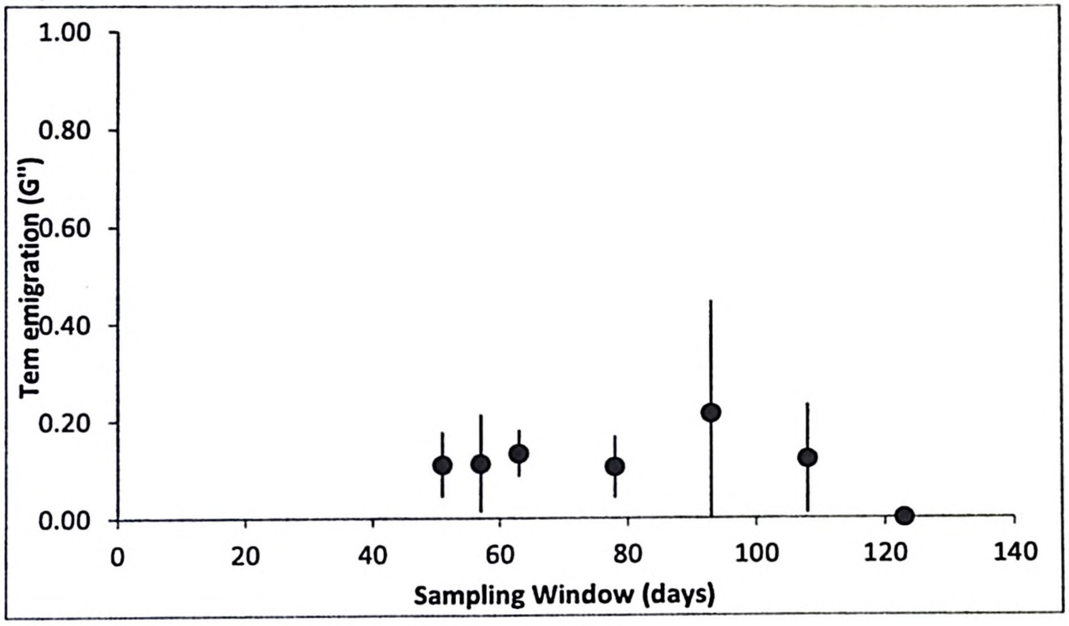
Sampling days	**Additions (recruitment intercept+ recruitment slope*sampling days)*100**	**Deletions (mortality intercept+ mortality slope*sampling days)*100**	**total change (additions +deletions)**
48	0.70	1.00	1.70
53	1.37	1.44	2.81
58	2.03	1.88	3.91
63	2.70	2.32	5.02
68	3.36	2.77	6.13
73	4.03	3.21	7.24
78	4.69	3.65	8.34
83	5.36	4.09	9.45
88	6.02	4.53	10.56
93	6.69	4.97	11.66
98	7.35	5.42	12.77
103	8.02	5.86	13.88
108	8.69	6.30	14.98
113	9.35	6.74	16.09
118	10.02	7.18	17.20
123	10.68	7.62	18.31

Figure 5.7: Graph showing population change (additions + deletions) from 48-120 days, i.e for a varying degree of population openess in Corbett National Park, 2012-2013



We found that temporary emigration probability was present irrespective of the length of the sampling window i.e, even if the sampling window is of 48-50 days, 15% of the individuals that were originally present might become unavailable by the end of the period (Fig. 5.8).

Figure 5.8: Graph showing temporary emigration (G'') against varying sampling days in Corbett National Park 2012-2013



6.5 Discussion

High density carnivore populations that are well connected with surrounding forests exhibit high turnover of individuals due to demographic processes like mortality, recruitment and temporary movements. This pattern has been observed through long-term camera-trap based monitoring of tigers in Corbett landscape, and entails profound implications of sampling duration on abundance estimates. Our aim is to characterize the relationship between sampling time and abundance, and explicitly understand the issues related to detection probability estimation and demographic processes that underlie this relationship. When we estimated abundance in increasing sampling window we found that the abundance and precision increase with increasing sampling window and this increase was drastic from 15-45 days than beyond it. Abundance estimate is derived from a canonical estimator which is the total number of photo-captured individuals divided by the detection probability.

When the sampling duration is very short the individuals with inherently low detection probability are not captured and hence the heterogeneity models are not able to account for this heterogeneity. Tiger individuals with inherent low capture probability do not appear in the sampling if the sampling window is very short (≤ 15days) which positively biases the detection probability estimation & negative biases abundance estimates. But when the sampling windows is very large the population becomes open to survival, recruitment and movement. Hence selection of sampling window is a trade-off between robustly estimating the heterogeneity in detection probability and yet not making the population geographically or demographically open. High probability of temporary movements as estimated in the present study cause violation of geographic closure. Hence, geographic closure is an unrealistic assumption and the population becomes open the moment sampling starts for a finite time period.

We developed an analytical framework that explicitly tests the change in population composition with time thereby we are able to choose sampling window which is a trade-off between robustly estimating detection probability and maintain tolerable level of population change (5%).The tiger conservation science is moving from one time estimates of abundance to long term monitoring of population and selecting an appropriate sampling window before setting up a monitoring project is of utmost importance as shown how abundance is affected by sampling duration.

Corbett Tiger Reserve is a high density source population (Bisht et al. 2019), such populations are characterised by high turnover rates and therefore a sampling window estimate from such a population that does not introduce bias in N-hat is likely applicable to all tiger populations since their turnover rates will likely be lower (except in the case of high mortality associated with poaching).The time frame for population estimation suggested by our study is between 40-55 days with a camera density of one camera per 2 km^2.

CHAPTER 6: FOOD HABITS AND SPACE USE BY TIGERS IN CORBETT NATIONAL PARK

6.1 Introduction

Shivalik and Terai on the Indian side harbor some of the densest tiger populations and hold high tiger prey numbers (Jhala et al. 2015). This region contiguous for over 15,000 km^{2}through connected forests that helps in maintaining tiger population in this area as a meta population complex. Yet, tiger ecology from this region of the world remains data deficient. Information on food habits and spatial distribution of tiger in the Indian Terai has been studied by Harihar et al. 2009, 2014 and Chanchani et al. 2016. Harihar et al 2009 and 2014 detail tiger food habits and distribution of tiger prey in the Rajaji - Corbett landscape while Chanchani et al. 2016 studied spatial distribution of tigers at the interface of various protection levels in Central Terai (Pilibhit Tiger Reserve, Dudhwa Tiger Reserve and Katarniaghat Wildlife Sanctuary). Most of our information on tiger food habits and home range are derived from the central or southern Indian population (Biswas and Sankar 2002, Majumdar et al 2016, Karanth and Sunquist 2000) where the habitat and prey assemblages are very different from the ones present in Shivalik and Terai.

Having basic knowledge about how a top predator utlises the prey and space in an area are important for furthering our knowledge on their ecology and also for the suggesting measures to combat their declining trend. Tigers are obligate carnivores that prey upon the largest ungulates in all the ecosystems in which they occur (Seidensticker, 1997). The average weight of species reported to be hunted by tigers is 60 kg (Sunquist et al 1999), although they are known to hunt prey varying from small mammals to the largest of the bovids and elephants (*Elephas maximus*) and one horned-Rhinoceros (*Rhinoceros unicornis*). In most of the tiger's range, major contribution to its diet is by cervids which make up to 75-80% of the prey biomass requirement of the tiger (Sunquist et al 1999). Food habits comprise one of the major determinants of various life-history strategies in carnivores including spacing pattern, movement, habitat selection, social structure, success of reproduction and geographical distribution (Krebs, 1978; Bekoff, Daniels & Gittleman, 1984; Sunquist & Sunquist, 1989). Our understanding of this phenomenon is far from complete (Sunquist & Sunquist, 1989) and especially from the Indian Terai, which has one of the highest tiger densities in the world. Thus, increasing knowledge of tiger food habits in such a place will enable us to recognize the plasticity in the predator's ability to use the available resources.

Tigers are solitary felids where males maintain home ranges that overlap with 2-3 females, while females are known to maintain exclusive home ranges that do not overlap with neighbouring females (Sunquist 1981, Smith et al 1987). Home range pattern of tigers is highly variable across their range and hence it helps throw light on their space requirements. Tigers are known to maintain small home ranges in prey rich alluvial flood plains of India and Nepal as compared to several hundreds of square kilometers in the cold, prey deficient climes of the Russian Far East (Smith et al 1984, 1987, Sunquist 1981, Goodrich et al. 2010). Size and structure of home ranges as well as spatial relationships of neighboring individuals have profound impacts on potential densities of a population, and, consequently, on the total space required for conservation (Naumov 1972; Shilov 1995). Spacing pattern of large carnivores can affect demographic parameters of populations and hence understanding spatial structure can provide insight into effective conservation strategies.

We studied food habits and spatial distribution of tigers in Corbett National Park from 2010-2015 from prey remains in tiger scat and intensive long term camera trapping respectively. We wanted to fill knowledge gap on tiger ecology from this region and see how a territorial large carnivore, like tiger, adjusts its space use and requirements when placed at high density.

6.2 Field Methods

6.2.1 Minimum range use

Radio collars are active detectors, while camera traps act as passive detectors and therefore not suitable for estimating home range as it is traditionally defined (Burt 1943). However, with high camera trap density and sufficient recaptures of individual tiger we can estimate a consistent unbiased index of short term home range or minimum usage area. For the current study we use only the resident population for our analysis. We defined resident females and males as the individuals that had been present in the study area for >= two years. Additionally, for females we considered individuals that were photo-captured as lactating/and or with cubs as residents as well. We used spatial camera trap based capture history of each individual (2010-2015) to estimate minimum range estimates for males and females. For estimating homerange overlaps I used the year long camera trap data (for details refer section 5.2, Chapter 5) since it provides a more in-depth understanding of temporal and spatial pattern of usage.

6.2.2 Food habits

The diet of carnivores can be ascertained from remains in their scats (Korschgen 1980) by quantifying the remains of the prey consumed for details of what it eats and how much it eats.

6.2.3 Prey availability

Prey density was estimated as part of another study on this project (Banerjee S. unpublished data), using line transect based Distance sampling (Bisht et al. 2012 and Jhala et al 2015). This data was made available for analysis of prey availability and preference for this objective.

6.2.4 Prey Utilisation

To estimate what proportion of prey was utilised with respect to its availability we collected tiger scat samples. Scat samples were collected from roads, trails and paths during sign surveys and opportunistically (2011-2014). During the collection of scats from field GPS locations was noted and scats collected in a paper bag (old samples) or a zip-lock (fresh samples). The samples were sun dried in field, individually labelled and brought to the laboratory (Wildlife Institute of India) for further analysis.

6.3 Analytical Methods

6.3.1 Minimum range use

For this analysis we first estimated the minimum number of captures required to estimate minimum usage area, by sub-sampling the capture history of individuals that had more than 3 spatial captures. We subsequently randomized these capture locations and estimated the minimum convex polygon (MCP) range (Mohr 1947) by sub-sampling recaptures in increments of three locations. We plotted the cumulative range area against increasing number of recapture locations to determine the number of locations where the range achieves an asymptote. The number of locations required per tiger for achieving this asymptote was considered as the minimum sample (recaptures) needed. All resident tigers whose capture history exceeded this minimum recapture number were used for estimating home range size.

Homerange overlaps: To determine if a female home range was used exclusively or not we defined neighbouring females as those that had adjacent and potentially overlapping home ranges during the same time period. As we did not have continuous data on this for all the females in the study area we used data from 100 sq km of the area that we camera trapped for 365 days. We used only the females and males photo-captured during this time to estimate overlaps in home range areas. For estimating proportion/ area of overlap between two home ranges, we used command "intersect" in ArcMap10, which gives overlap/intersected area between two polygons (in this case MCP). We then estimated minimum percentage overlap , defined here as HRij = Aij/Ai, where HRij is the proportion of individual i's home range that is overlapped by individual j's home range, Ai is the area of individual i's home range and Aij is the area of overlap between the two individuals' home ranges (Kernohan et al., 2001).

Homerange shifts: To see if a tiger individual had shifted its homerange over the years we calculated weighted homerange centroid using captures of tiger individuals in ArcMap10. If the difference between yearwise centroid was more than its homerange radius, which was estimated as 1.1 km for females and 2.1 for males (details see table 4, Chapter 3), then it was recorded as a shift in homerange.

6.3.2 Food Habits

There is no definitive morphological basis of segregating leopard and tiger scats (Jhala pers comm), therefore for food habits study it is important to establish the origin of scat through other means. Hence, for establishing species identity from the scat, we used molecular based analysis, therefore scats collected from field in plastic zip pouches containing silica were later aliquoted and kept in -20 °C freezer in 2ml screw cap vials/double bagged zip pouches with silica gel. Corbett Tiger Reserve had very few leopards (*Panthera pardus*) and these were primarily restricted to the periphery of the park (Jhala 2014 unpublished data). For scats that could not be genetically identified, to avoid confusion with its major co-predator, leopard, wediscarded scats collected from area where we had information on leopard presence *viz.* our camera trap photo records, sign survey data, direct sighting and informal local interviews. Washed samples of hairs from the scats were passed through ether and xylene (Koppikar & Sabins 1975) for 15-20 minutes to induce transparency. The hairs were then mounted on a slide using Canada balsam or DPX mount and examined under microscope with 10x and 40x resolutions. At least 20 hairs were examined from each scat (Mukherjee *et al.* 1994) and prey species identified by comparing it with the reference slides/samples available at Wildlife Institute of India.

6.3.3 Prey Availability

The data was analysed using program DISTANCE 5.0 (Buckland et.al, 1993, 2001; Thomas et.al, 2004). The best model fitting the data was selected based on the Akaike Information Criteria (AIC). Using the selected model, estimates of group density, animal density were derived by pooling data for all walks for a given transect.

6.3.4 Prey Utilisation

6.3.4.1 Frequency of Occurrence of Prey in Carnivore Diet

Frequency of occurrence of a prey in carnivore diet is the percentage of total scats in which a particular prey species is found. It indicates how common an item is in the diet of that particular carnivore (Ackerman *et al.* 1984). This gives us an idea of diet stabilization of the scats *i.e.* minimum number of scats required for estimating predator species diet (Jethva & Jhala 2003).

6.3.4.2 Percent Occurrence of Prey in Carnivore Diet

Percent occurrence of prey species is number of times it is found as percentage of all items found in the carnivore diet. It provides a better indication of the relative frequency than frequency of occurrence with which each item is consumed because it accounts for more than one of a given item being found in a scat (Ackerman *et. al.* 1984).

6.3.4.3 Prey Biomass consumed

The frequency of occurrence is a measure of prey intake and composition. However, if the body sizes of different prey items are highly variable, frequency of occurrence can be a misleading metric because of the surface to volume ratio problem (Floyd *et. al.* 1978, Ackerman *et. al.* 1984). Because of their relatively greater surface area in relation to volume in smaller prey species, their consumption results in the production of relatively more scats compared with larger prey species. This leads to an overestimation of the proportion of small prey and underestimation of large prey in predator diet profiles when the frequency of occurrence is used as a measure. To overcome this problem, the frequency occurrence of each prey item in tiger scatswas converted to biomass consumed, by Chakrabarti *et al.* 2016, where biomass consumed per collectable scat scaled to carnivore weights (Y) showed an asymptotic patterns against prey weight (X):

Biomass Consumed per collectable scat / carnivore weight=0.033 -0.025exp$^{-4.284X}$

6.3.5 Prey preference

We used Ivlev's electivity index (Ivlev 1961) to look into prey preference by tigers in CTR. The purpose of the index is to characterize the electivity, or degree of selection, of a particular prey species by the predator being studied. The relationship is defined as

$$E = U - A / U + A$$

where E is the measure of electivity, U- Biomass consumed of the prey species and A-available biomass of the prey species. Biomass consumed is estimated from scats and available biomass using estimate of abundance and density from line transect based distance sampling. The index ranges from -1 to + 1, with negative values indicating avoidance or inaccessibility of the prey item, zero indicating random selection from the environment, and positive values indicating active selection.

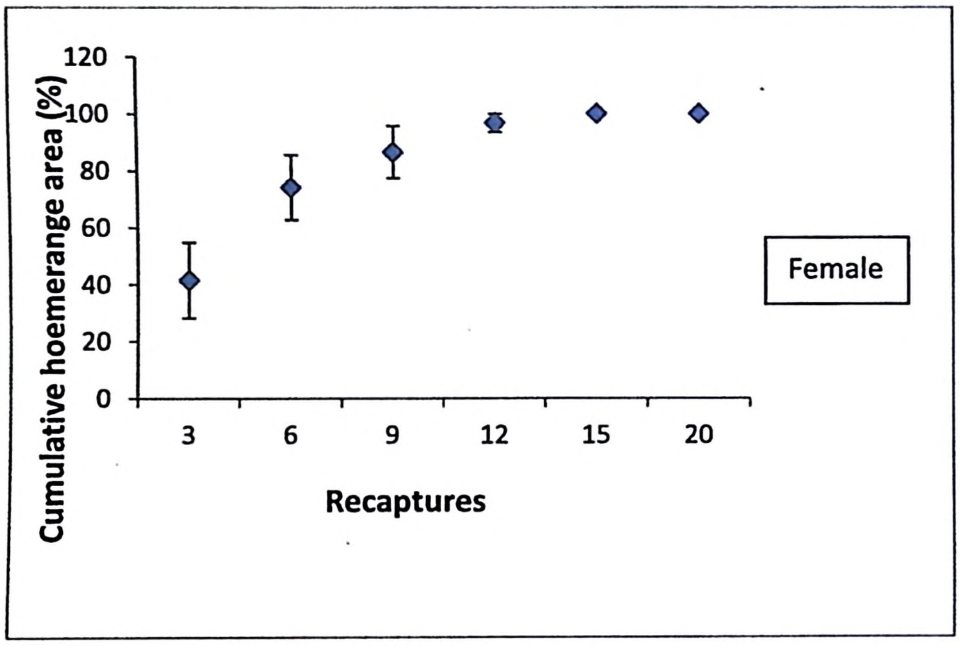
6.4 Results

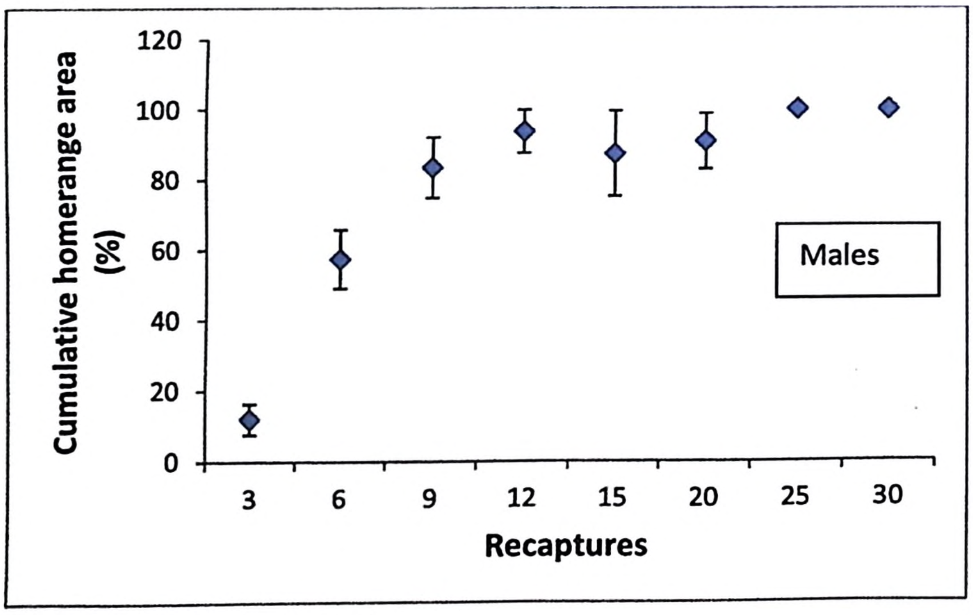
6.4.1 Minimum range use

From our six year data we had six females and 12 males that had more than 20 photo captures in a year. Cumulative home range estimates for females reached an asymptote after 9 captures and for males at 12 captures (Fig.6.1). Using this criteria we estimated home range of females (n=31) at 3.1 $\pm$ 0.5 km^2 and for males (n=38) at 10.6 $\pm$ 1.1 km^2.

When we estimated annual homerange of only the resident individuals we found that average annual homerange of males (n=15) increased to 16.4 ± 1.6 km^2, while that of females (n=14) remained the same at 3.9 ± 0.8 km^2. Average annual homerange area for lactating females (n=8) was 3.1 ±0.8 km^2.

Figure 6.1: Cumulative homerange area (%) for females (n=6) and males (n=12) plotted against increasing number of recaptures to reach an asymptote





6.4.1.1 Overlaps and Stability of home ranges

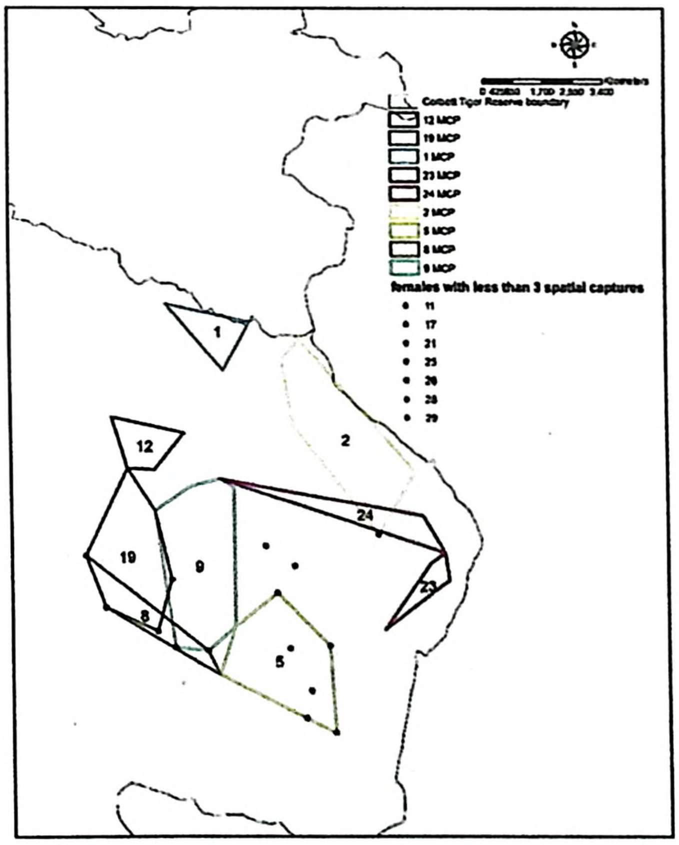
Of the 13 long term resident females we found that none of the females home range centroid changed over the years. In the year long study we photo-captured 16 females and of those only 5 had overlapping homeranges (Fig.6.2). The average overlap percentage was 16 ± 8% km^2 and area of overlap between 5 overlapping female individual ranged between 0.2 to 1.5 km^2 (Table 6.1).

Table 6.1: Minimum homerange area (MCP) and overlap area between females (n=5) in Corbett Tiger Reserve, 2012-13

ID1	ID2	MCP_ID1 (km^2)	MCP_ID2 (km^2)	HR$_{12}$ (km^2)	HR$_{21}$(km^2)	overlap (km2)	Avg overlap (%)
24	2	8.6	2.6	0.05	0.15	0.4	10
19	8	6.6	2.5	0.23	0.60	1.5	41
19	9	6.6	8.6	0.03	0.03	0.22	3
9	8	8.6	2.5	0.04	0.12	0.31	8

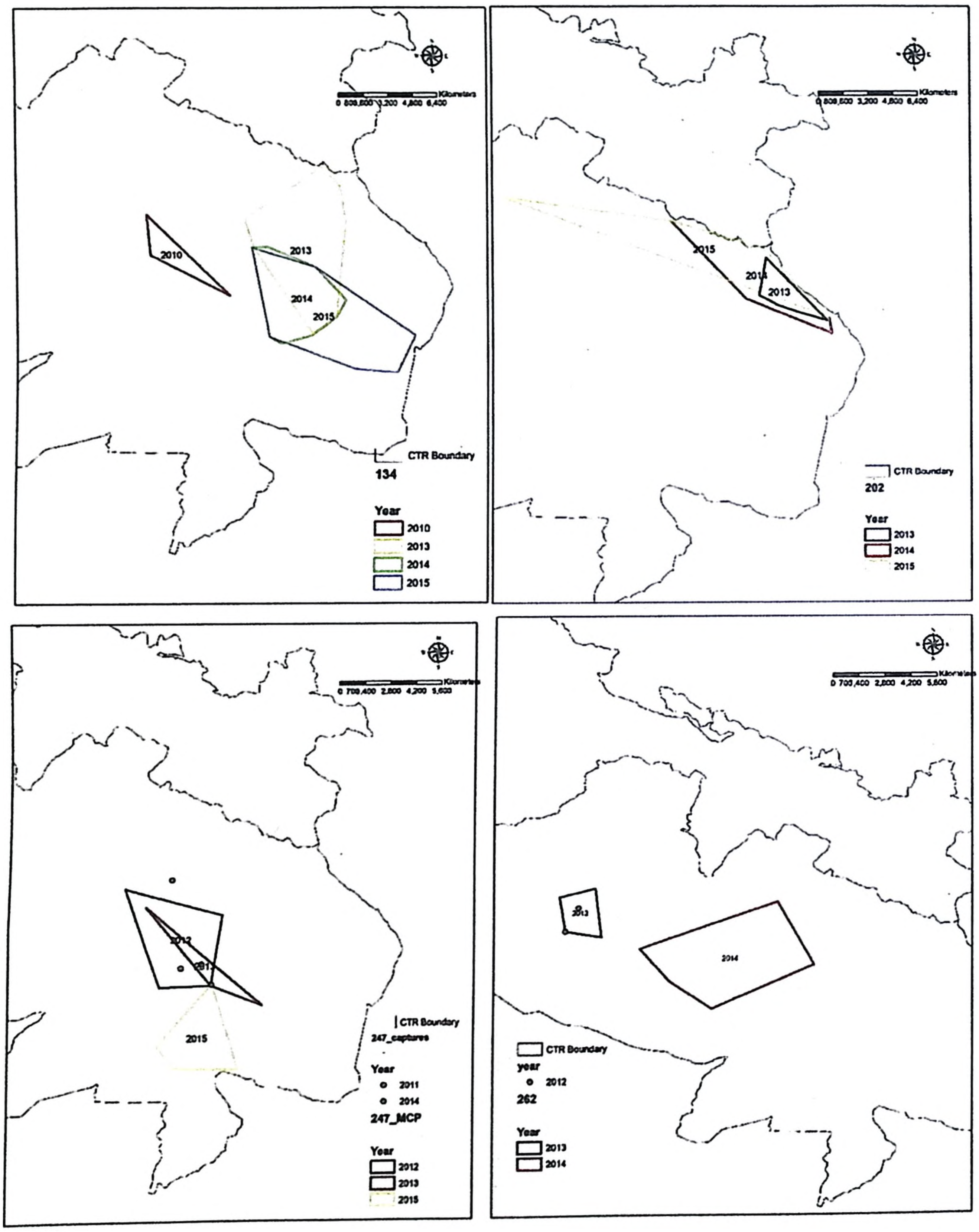
ID1 and ID2: tiger individual IDs; MCP: Minimum Convex Polygon as surrogate for the minimum homerrange area; HR$_{12}$: the proportion of animal ID1's homerange that is overlapped by animal ID2's home range; HR$_{21}$: the proportion of animal ID2's homerange that is overlapped by animal ID1's home range

Figure 6. 2: Map showing spatial distribution and minimum home range area of females (n=16) in Corbett Tiger Reserve 2012-13



Of the 15 resident males in the study area, 4 males had shifted their home ranges in the 6 years of study period (Fig. 6.3).

Figure 6.3: Map showing homerange areas of males (n=4) whose homerange centroid changed from 2010-2015 in Corbett Tiger Reserve.



We photo-captured 9 males in our yearlong study and 8 of them had overlapping homeranges. The overlap percentage of males was 31±4% and area of overlap ranged from 1.5 km^2 to 15 km^2 (Table 6.2).

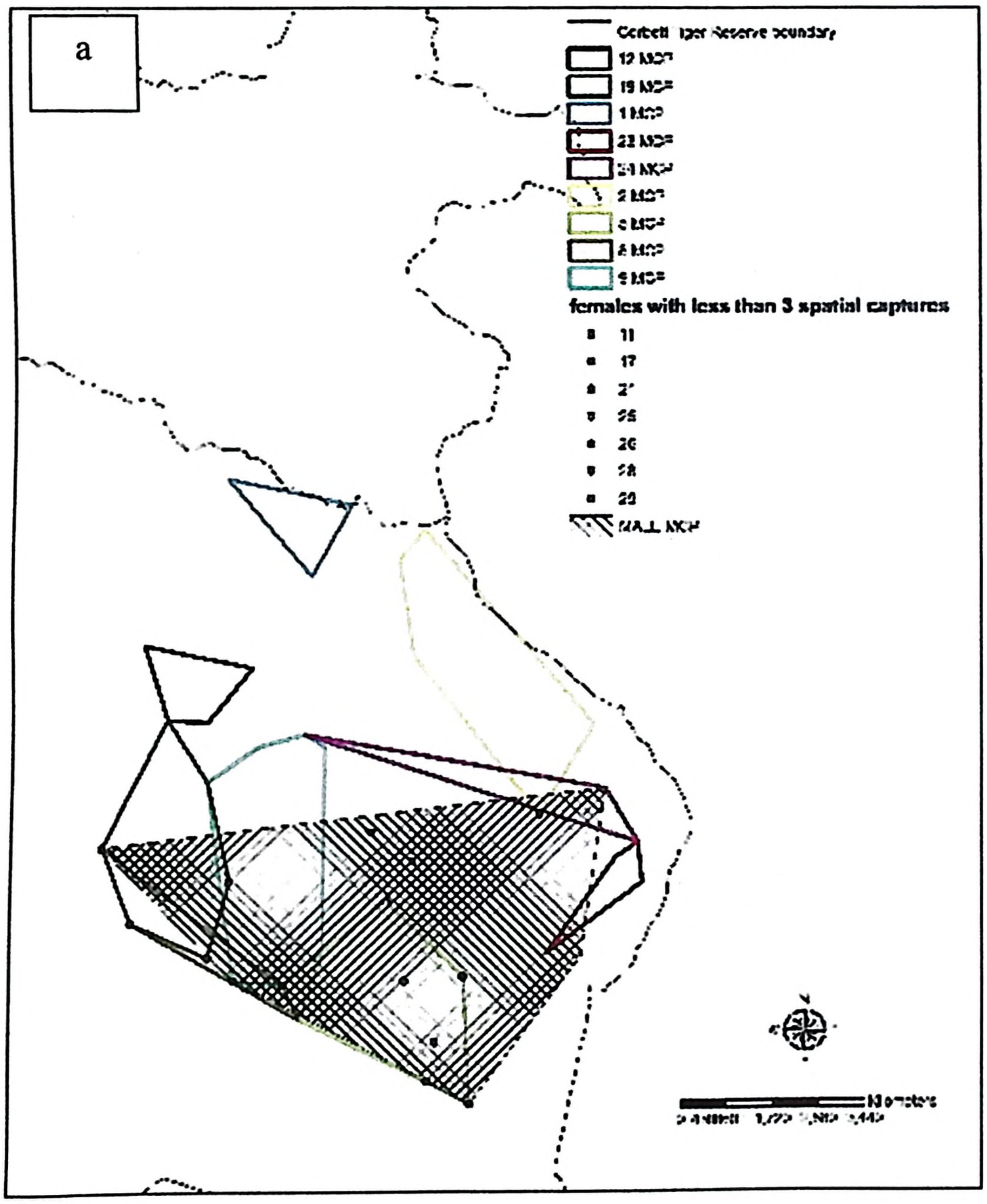
Table 6.2: Minimum homerange area (MCP) and overlap area between males (n=8) in Corbett Tiger Reserve, 2012-13

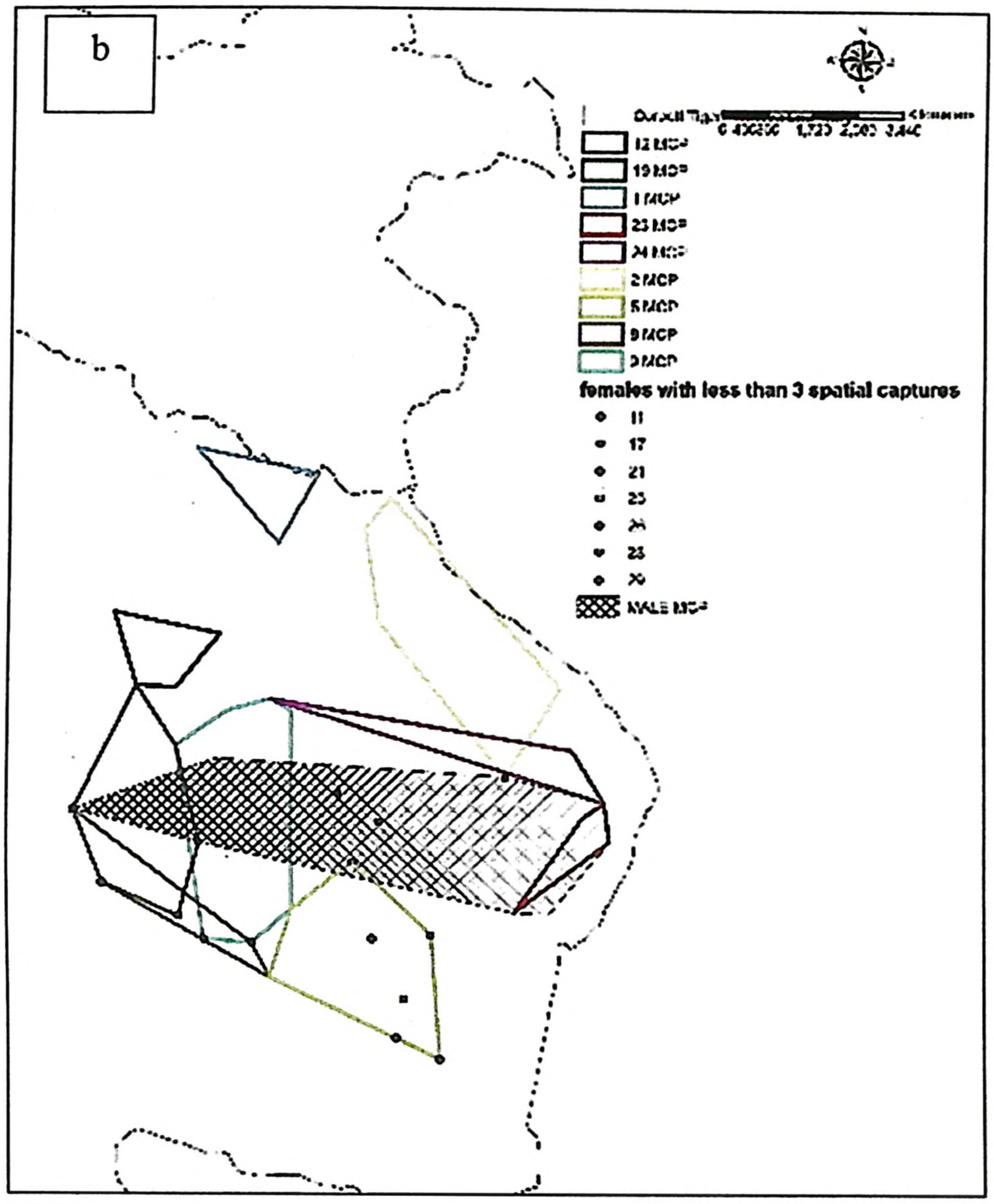
ID1	ID2	MCP_ID1 (km^2)	MCP_ID2 (km^2)	overlap (km^2)	Avg overlap (%)	HR_{12} (km^2)	HR_{21}(km^2)
13	14	8.32	18.34	1.47	13	0.18	0.08
13	18	8.32	17.8	8.1	71	0.97	0.46
13	20	8.32	18.7	5.32	46	0.64	0.28
13	3	8.32	32.96	3.26	25	0.39	0.10
13	4	8.32	27.8	1.39	11	0.17	0.05
13	7	8.32	40.83	7.89	57	0.95	0.19
14	18	18.34	17.8	1.7	9	0.09	0.10
14	20	18.34	18.7	6.5	35	0.35	0.35
14	27	18.34	24.47	3.13	15	0.17	0.13
14	3	18.34	32.96	14.81	63	0.81	0.45
14	4	18.34	27.8	5.74	26	0.31	0.21
14	7	18.34	40.83	2.67	11	0.15	0.07
18	20	18.26	18.7	6.62	36	0.36	0.35
18	3	18.26	32.96	4.28	18	0.23	0.13
18	4	18.26	27.8	2.73	12	0.15	0.10
18	7	18.26	40.83	17.8	71	0.97	0.44
20	3	18.7	32.96	11.38	48	0.61	0.35
20	4	18.7	27.8	13.67	61	0.73	0.49
20	7	18.7	40.83	8.6	34	0.46	0.21
27	3	24.47	32.96	3.35	12	0.14	0.10
27	4	24.47	27.8	5.82	22	0.24	0.21
3	4	32.96	27.8	8.72	29	0.26	0.31
3	7	32.96	40.83	5.42	15	0.16	0.13
4	7	27.8	40.83	4.68	14	0.17	0.11

ID1 and ID2: tiger individual IDs; MCP: Minimum Convex Polygon as surrogate for the minimum homerrange area; HR_{12}: the proportion of animal ID1's homerange that is overlapped by animal ID2's home range; HR_{21}: the proportion of animal ID2's homerange that is overlapped by animal ID1's home range

In terms of male and female homerange overlaps, males homeranges overlapped 3 to a maximum of 7 females (Fig 6.4). Two females had only one male overlapping its home range while the other females had multiple males homeranges overlapping theirs.

Figure 6. 4: Maps (a-h) showing homerange overlaps of males (n=8) with females (n=16) in Corbett National Park, 2012-13

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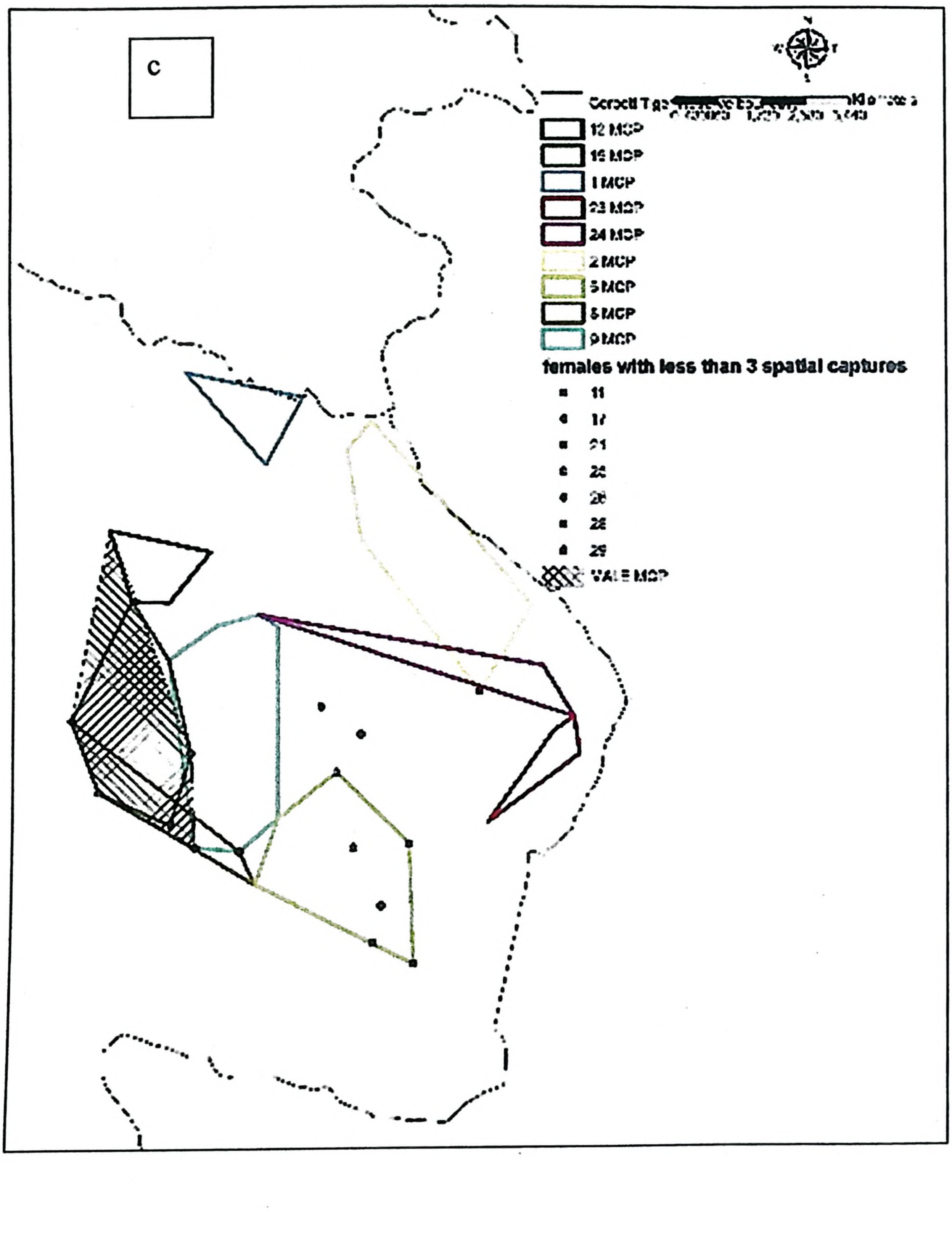
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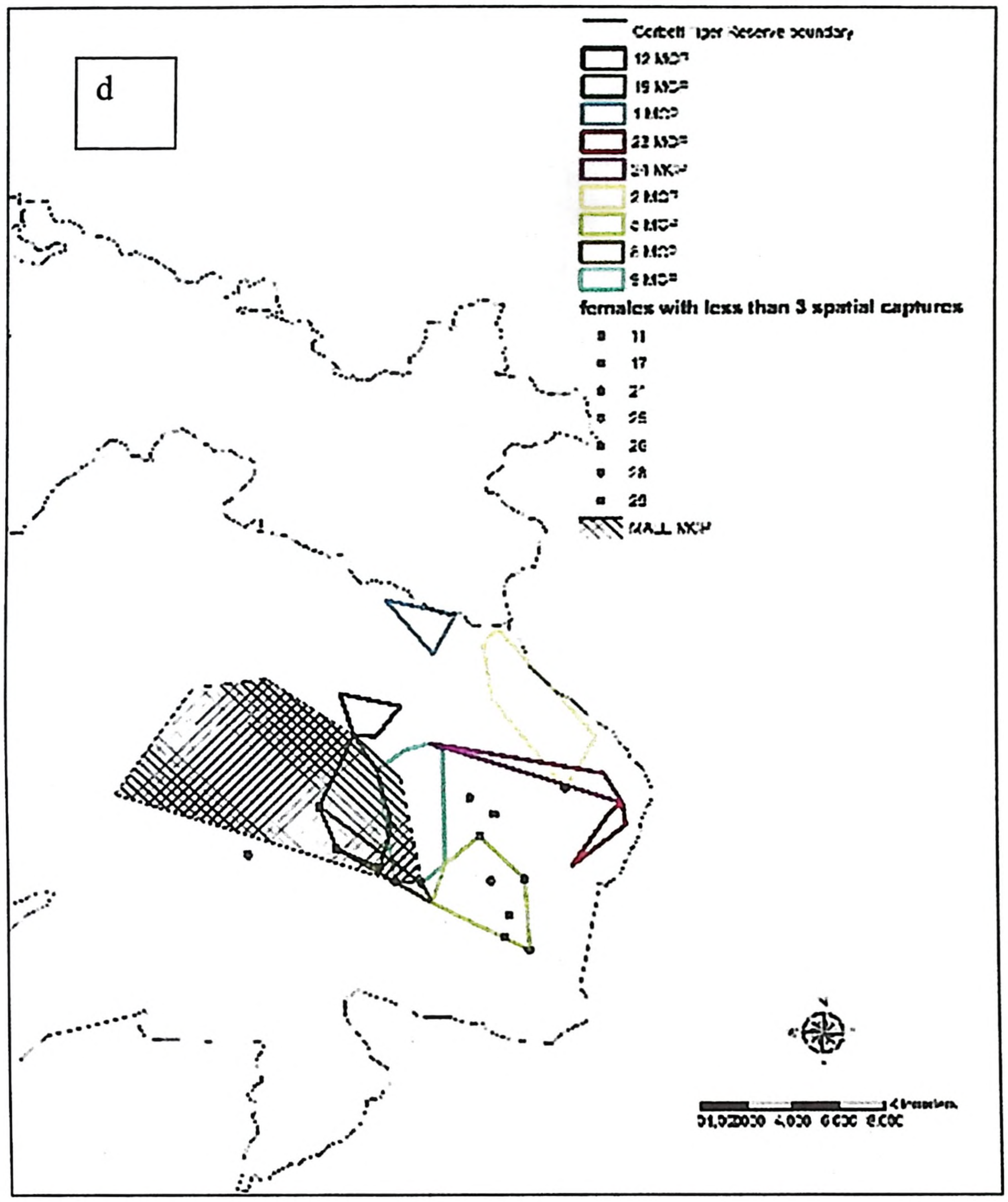
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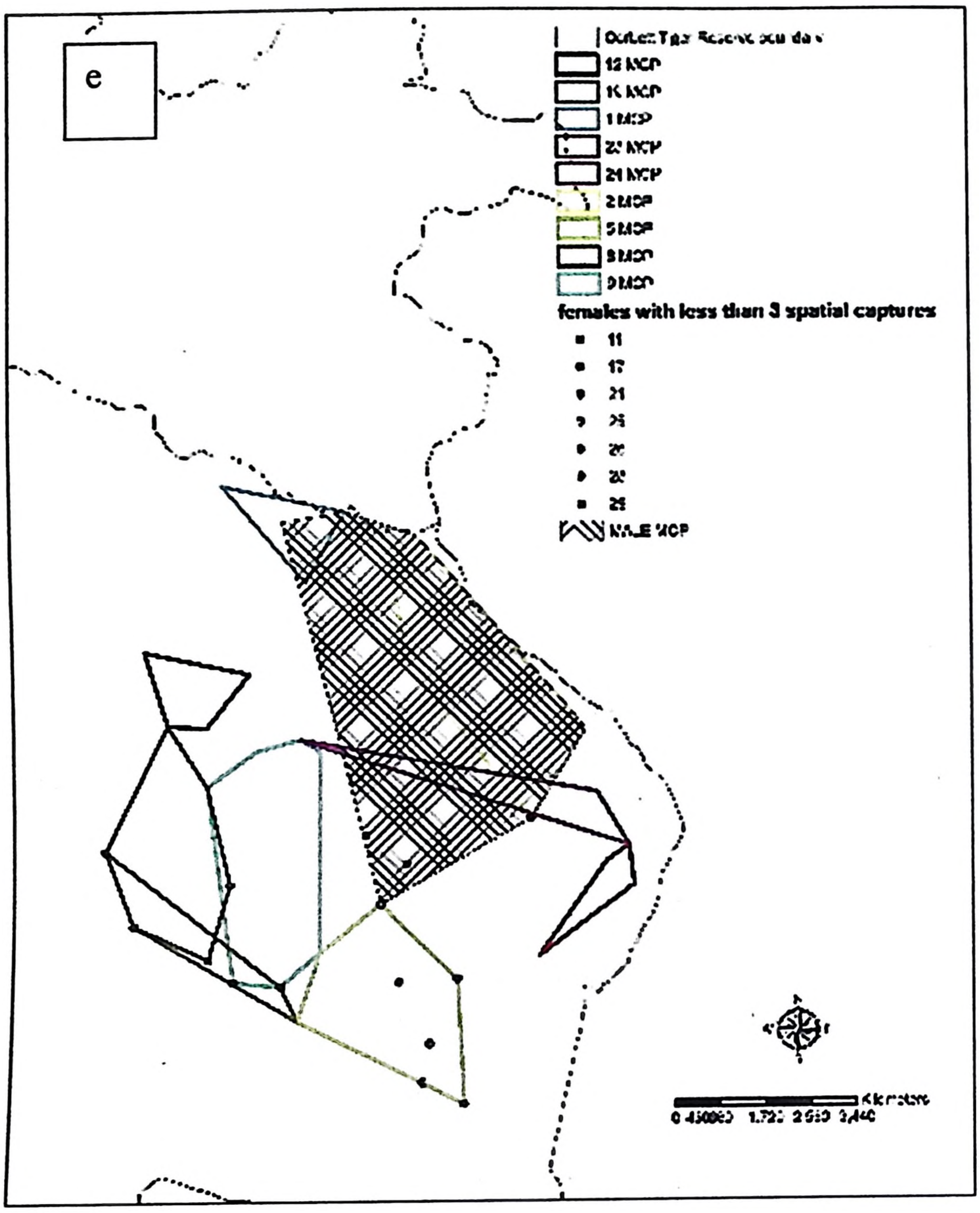
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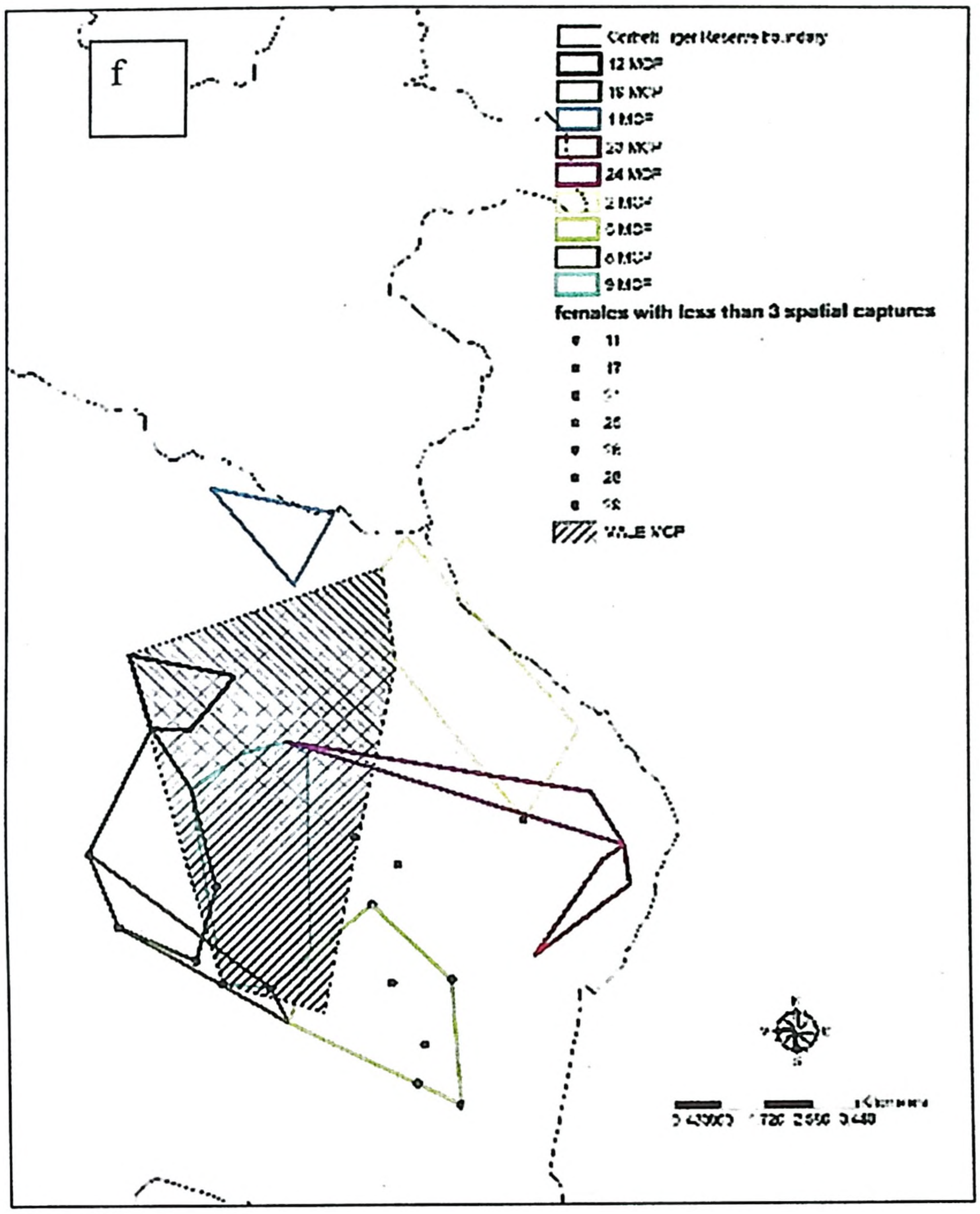
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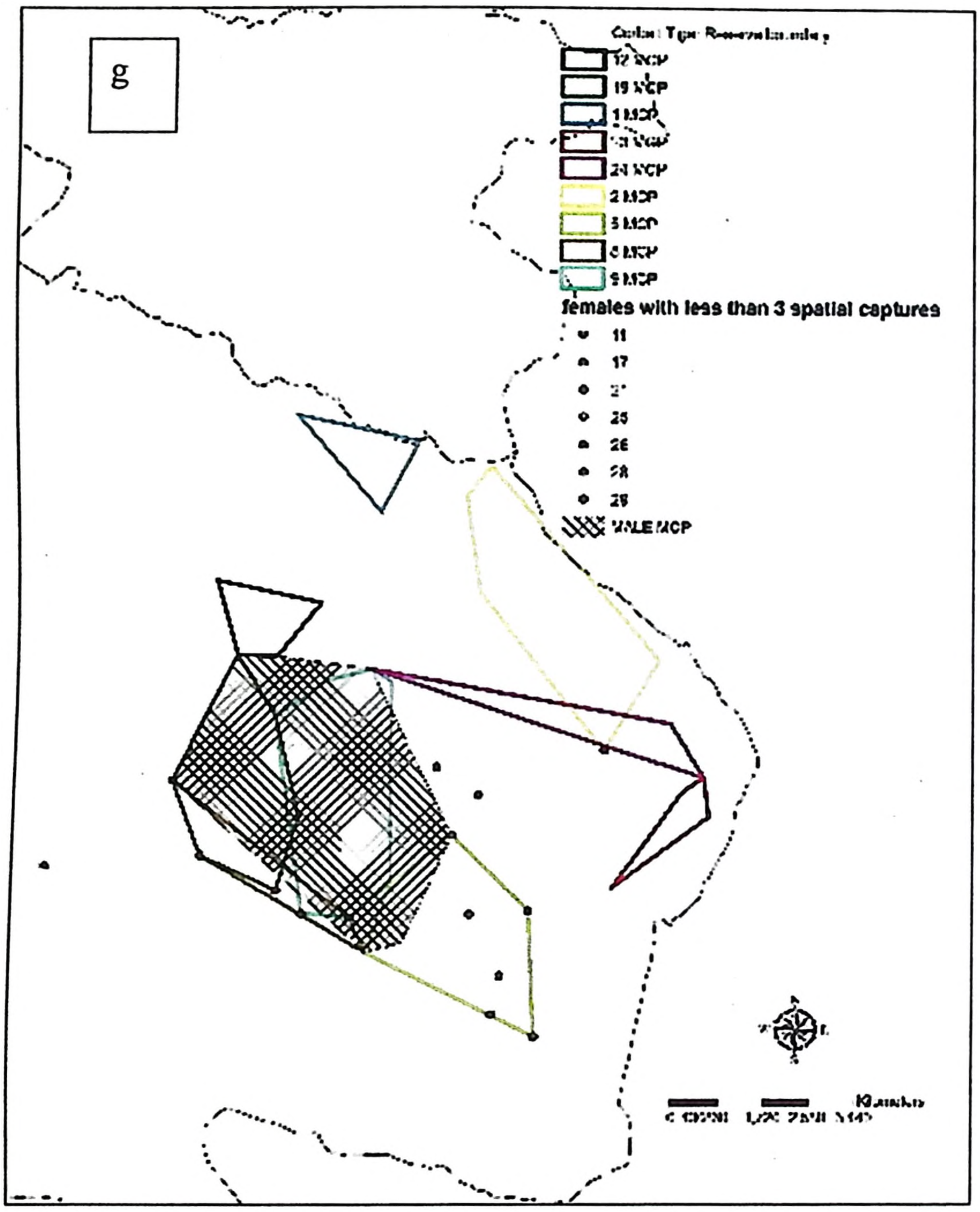g
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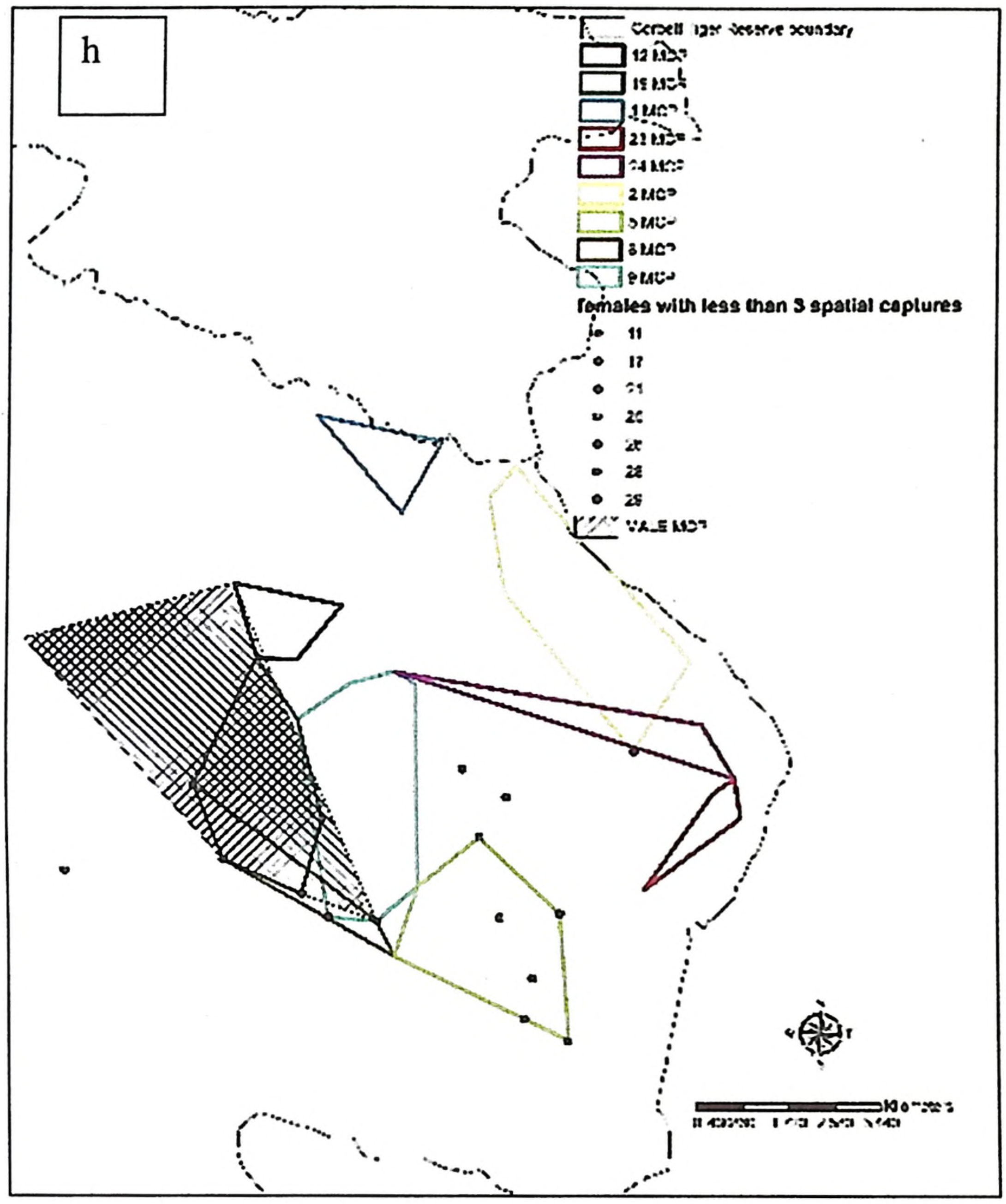

h
Corbett Tiger Reserve boundary
12 MCP
15 MCP
1 MCP
23 MCP
24 MCP
2 MCP
5 MCP
8 MCP
9 MCP
females with less than 3 spatial captures
11
17
21
20
25
28
29
MALE MCP
Kilometers

6.4.2 Food Habits

Analysis of 79 scats revealed presence of six prey species with a high preponderance of medium-sized to large sized ungulates in the tiger's diet. chital, sambar and barking together accounted for 91% of all prey consumed, while domestic livestock contributed 2.5%. No remains of wild pig and elephant were found in tiger scats.

6.4.3 Prey availability

Results for the prey density estimates by Banerjee S. (unpublished data) are provided in (Table 6.3). Banerjee S. (unpublished data) recorded highest encounter rate (0.53 per km walk) for chital amongst the prey species followed by sambar (0.26 per km walk). The most sighted prey was chital (n= 826) followed by sambar (n=402). The two primary prey of tiger, chital and sambar had a density of 76 per km2 and 9 per km2 respectively (Table 6.3).

Table 6. 3: Density of major tiger prey computed from 309 transects each of 2-3 km length with an effort of 1543 km using program DISTANCE 5.0,Corbett National Park between 2010-15 (Banerjee S. unpublished data)

Species	N	n/L	SE	ESW	SE	p	DS	SE	E(S)	SE	D	SE
Chital	826	0.53	0.03	36.90	0.96	0.2	7.25	0.48	10.50	0.45	76.15	6.02
Sambar	402	0.26	0.02	38.40	1.24	0.3	3.39	0.25	2.71	0.09	9.20	0.74
Barking Deer	196	0.13	0.01	32.33	2.64	0.4	1.96	0.24	1.46	0.04	2.86	0.36
WildPig	108	0.07	0.01	35.06	2.51	0.5	1.00	0.13	6.41	0.63	6.40	1.07
Langur	159	0.10	0.01	35.97	3.21	0.4	1.43	0.21	11.35	1.15	16.24	2.93

N- Number of clusters sighted; n/L- encounter rate per km walked; ESW- Effective Strip Width; P-hat – Detection probability; D(S) – Density of groups ;D-Density of individual ; E(S)-Group size

6.4.4Prey Utilisation

6.4.4.1Frequency of occurrence

Chital was the most frequently occurring prey species in tiger diet followed by Sambar and Barking deer (Fig. 6.5). The number of scats required was found to be adequate, where an asymptote was reached at around 60 tiger scats (Fig 6.5).

Figure 6. 5: Cumulative frequency of occurrence of prey (n=6) remains in tiger scats (n=79) in Corbett National Park 2010-15

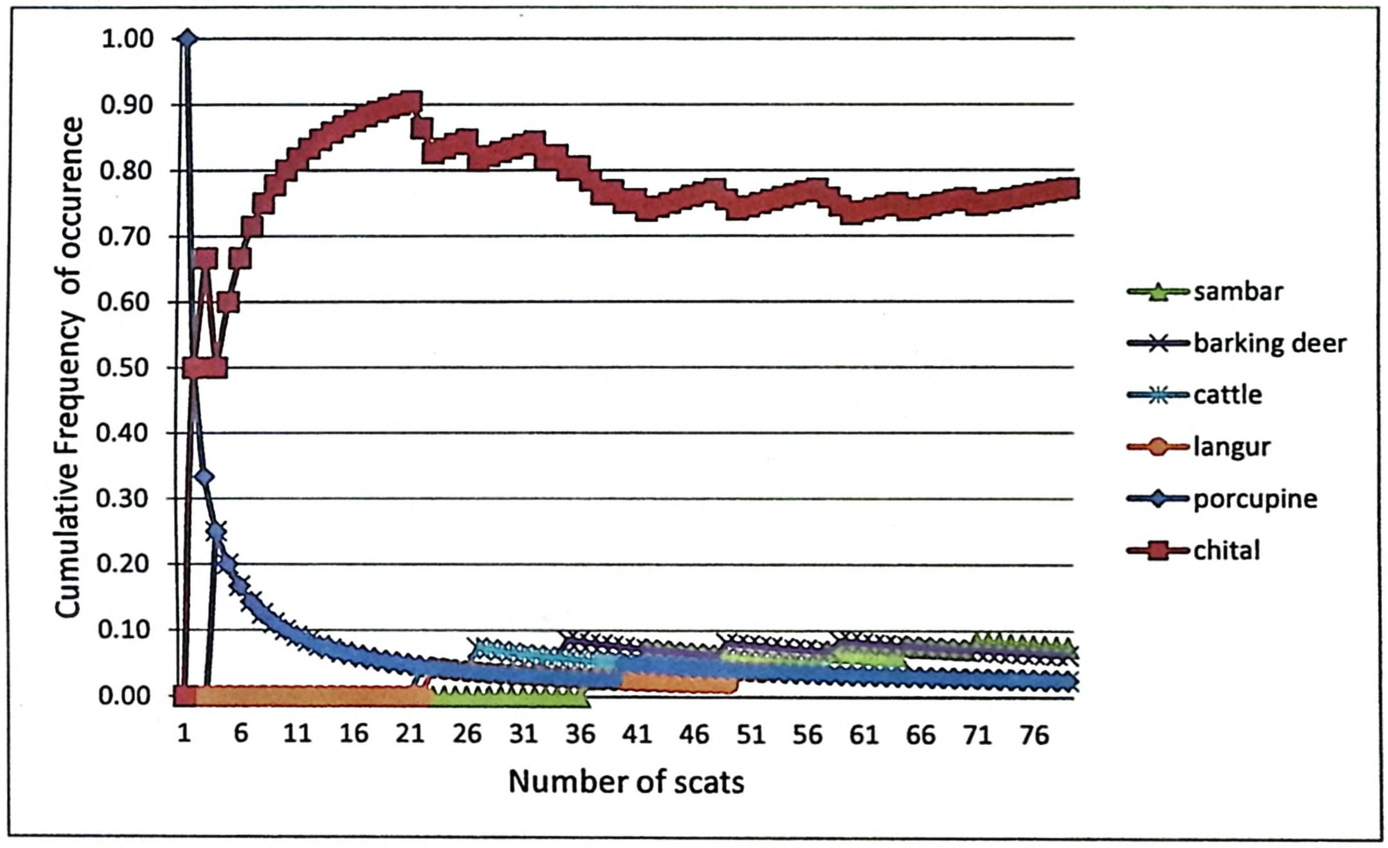
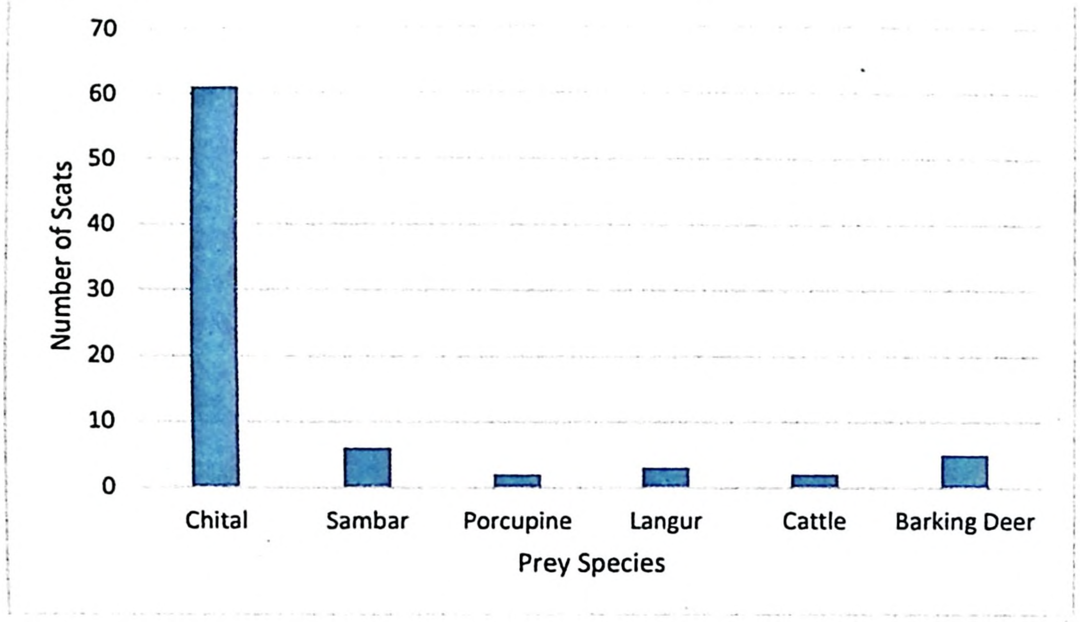


Figure 6.6: Occurrence prey species in tiger scat (n=79) in Corbett National Park, 2010-2015



6.4.4.2 Percent Occurrence prey species

Not all the remains in the scat could be identified. Claws, hairs, feathers and grass or leaves were not identified and thus were not included in the analysis. Moreover, these unidentified items formed minor proportion (less than 5%) of the prey remains in scats. All the 79 scats that were analyzed had only one prey item in it.

6.4.4.3 Prey biomass consumed

To estimate biomass consumed by tiger to produce one collectible scat we need predator and prey mass. For this we used prey and predator mass as reported in Hayward et al 2007, Mondal et al. 2011 and Awasthi et al 2016, which is 3/4th of the average weight of the female of the species (Table 6.4). Multiple prey items can be present in one scat, therefore we recorded the percentage with which different prey items were represented in one scat to estimate whole scat equivalent value. Since each scat contained only one prey item in the current study, the whole scat equivalent for a species was same as the number of scats in which the species was present.

Amount of biomass that needed to be consumed to produce one collectible scat was more for large bodied prey species like Sambar and Cattle (table 6.4). Chital contributed 82% to the diet of tiger followed by sambar and barking deer (table 6.4).

Table 6.4: Prey Biomass Consumed by tigers in Corbett National Park 2010-15

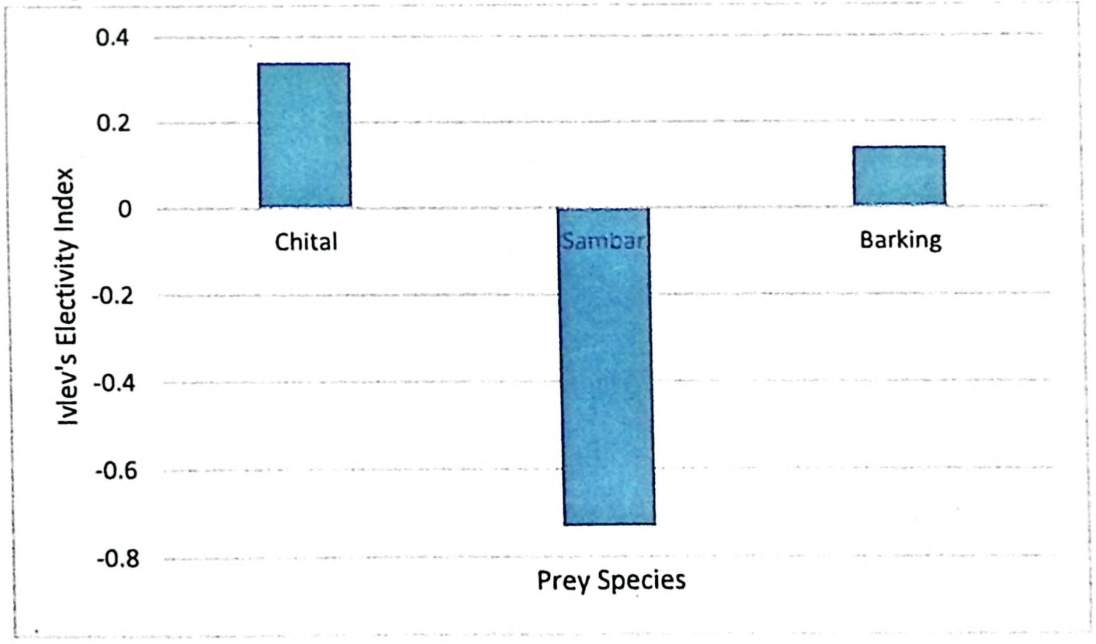
Prey	Prey Mass (kg)	Tiger Mass (kg)	Biomass (kg) per scat	WSE	Biomass consumed (kg)	Percent Biomass (%)
Chital	47	98	2.92	61	178.12	81.76
Sambar	136	98	3.22	6	19.36	8.88
Barking deer	18	98	2.11	5	10.59	4.86
Cattle	180	98	3.23	2	6.46	2.96
Porcupine	10	98	1.65	2	3.30	1.51

Prey and predator Mass: body weight of the tiger and its prey in Kg estimated as 3/4th of the female body wieght from literature (Mondal et al. 2011, Awasthi et al 2016, Hayward et al. 2007); **Biomass/scat (kg):** Biomass consumed per scat estimated as ((0.033-(0.025*EXP(-4.284*(Prey mass/Tiger mass))))*Tiger mass; **WSE:** whole scat equivalent; **Biomass Consumed (kg):** whole scat equivalent* Biomass/scat; **Percent Biomass (%):** this is biomass consumed calculated as Biomass consumed /sum of Biomass consumed)*100

6.4.4.4Prey preference

Ivlev's electivity index showed that chital was preferred while sambar was utilized less than available (Fig. 6.7).

Figure 6.7: Biomass consumed and available of prey species present in tiger diet along with index of electivity for the prey species (Ivlev's index)



6.5 Discussion

During our study (2010-15) we recorded 130 females, of which we identified 61 (~50%) to be residents since they were photo captured in 2 or more primary periods compared to 38% males, this indicated high site fidelity amongst females. Annual minimum usage areas of the breeders/residents was smaller than the annual home range areas recorded for tigers (see Sunquist 1981, Simchareon et al. 2014 and Chundawat et al. 2016). Females in Corbett showed high overlap (16%) with each other, as compared to 3- 9% overlap reported from central India, Nepal and Russia (Smith et al 1987, Goodrich et al 2010 and Chundawat et al 2016). Smaller homeranges and higher overlap among resident females suggests adjustment in space in response to high competition. Male home ranges were 3 times larger than those of females, which is similar to other studies in Asian forests (Smith et al 1987, Karanth & Sunquist 2000 and Naha et al. 2017). Overlap between males was high (31%) and their home ranges overlapped with 3-7 sympatric females. Many studies have documented male felid home-range sizes much larger than expected based on energetic demands, suggesting that other factors such as maximizing breeding opportunities influence male home-range size and degree of exclusivity (Sandell 1989).

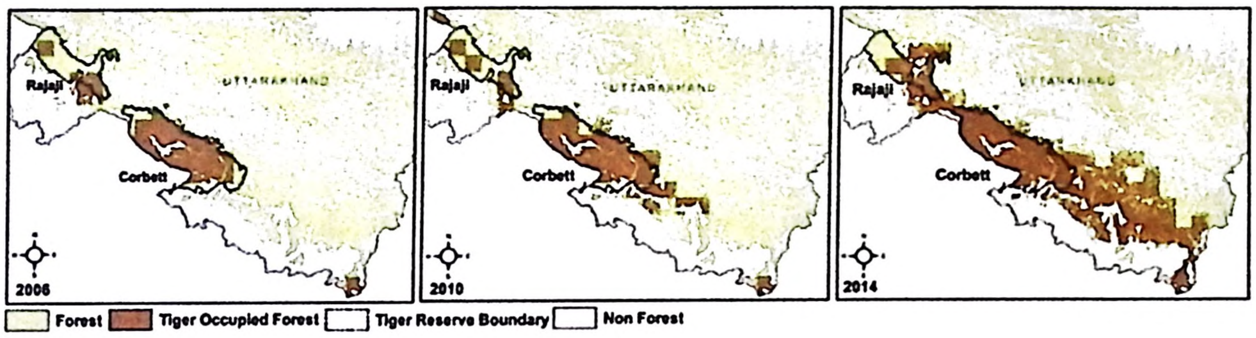
Males showed contraction, expansion and shifts in their usage area over the years, which was expected and two of the males were sub-adults who later established their territory and were photo-captured with breeding females in the new area. Contrary to this none of the females showed shift in homerange centroid in the study area. This again shows high site fidelity amongst females. In similar forests of Nepal where both tiger and prey densities are high, both male and female tigers maintain largely exclusive home ranges (Smith et al. 1987; Sunquist 1981), which was not observed in the current study.

Results from scat analysis showed that selective predation by tigers was directed towards prey species of medium and large body mass. Though Karanth & Sunquist (1995) found selective predation of tigers towards large-bodied prey in South India, they did not notice the same preference for medium-sized prey as seen in the present study. Cervids accounted for 91% of the prey species consumed by tigers in Corbett. This pattern is corroborated by findings from other studies on the food habits of tigers (McDougal, 1977; Sunquist, 1981; Johnsingh, 1983; Karanth & Sunquist, 1995; Stoen & Wegge, 1996) where cervids contributed on average up to 75% of the total prey intake of tigers (Sunquist et al., 1999). Chital in the study area contributed maximally to the diet of tiger and was consumed in proportion to its availability. Earlier studies (Johnsingh, 1983; Karanth & Sunquist, 1995; Stoen & Wegge, 1996) have reported an under use of this prey species by tigers when compared to its availability. In Corbett, chital occurs in higher densities than in other areas, which might have increased their encounter rate with the predator, eventually increasing the chance of predation. Sambar formed the second most important prey species for tigers in our study site, and was consumed in excess of its availability. When compared to studies from other areas, the predation rate on this species by tigers was relatively higher in Central India and South India (Schaller, 1967). All the sites where predation on sambar was more than Corbett indicate a correspondingly lower degree of chital predation by tigers.

CHAPTER 7: CONCLUSION

Prior to 2006, tiger populations were estimated by unreliable means (Karanth *et al.* 2003) and the official tiger estimate for India was 3642 tigers (Narain *et al.* 2005). Subsequent to the local extinctions of Sariska and Panna tigers caused due to poaching in 2005 and 2009 (Check 2006; Gopal *et al.* 2010) the first tiger status estimation based on modern scientific approach (such as the current study) was implemented and put the population at a precariously low number of 1411 (se range 1165-1657; Jhala *et al.* 2008). At that time camera trap study in Corbett National Park (2006-07) estimated the population to be at 108 (SE 4.5) within the same area of 500 km^2 (Contractor 2007) as the current study. The abundance estimate was within one standard errors of the estimates of the current study, indicating long term stability. Corbett was identified as one of the few sources of tigers remaining within the country and was prioritized for conservation investment (Jhala *et al.* 2008). By 2012 the entire Corbett Tiger Reserve (1288 km^2) had a tiger density comparable to that of the Corbett National Park, CTR being home to about 143-198 tigers (Bisht *et al.* 2012). This strategy of high investment in a source population has paid dividends and resulted in an increase in tiger occupancy and numbers in the larger landscape of western *Terai* between 2006 to 2014 (Fig. 7.1), where tigers have increased from 178 (SE 17) individuals occupying 1901 km^2 to 340 (SE 41) individuals occupying 6576 km^2 (Jhala *et al.* 2008, 2010, 2014).

Figure7. 1: The Terai landscape was sampled for tiger signs by a 15 km search within each 15 km^2 forested patch as part of the occupancy survey for national tiger status evaluation (Jhala et al., 2008, 2011, 2015). Forest patches where tiger sign were detected are marked in brown. Expansion in tiger occupancy from Corbett Tiger Reserve across western Terai landscape is clearly seen from 2006 to 2014.



The high density source population of Corbett National Park was characterized by a stable population with high proportion of breeding females, high recruitment, low survival and high turnover of individuals. These characteristics permitted tigers to be produced at rapid rates to disperse and populate all available habitat within the landscape within a period of eight years. The optimal *Terai* and foothill habitats were almost all occupied by tigers by 2014, and tigers are now dispersing to high altitude habitats as well (Bhattacharya and Habib 2016). Our study documents potential thresholds that can be achieved by tiger populations under optimal conditions. This information and the strategy of focusing conservation efforts on source populations within each landscape can be used to plan and implement realistic tiger recovery programmes globally.

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APPENDIX

Table S.1: Model selection statistics for robust design analysis of Block I tiger capture data from Corbett National Park, India, 2010–2015

Sno	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num . Par	Deviance
1	$S_{(.)}G''_{(0)}G'_{(1)}pi_{(ct)}p_{(.)}c_{(.)}$	5235.4205	0	0.58185	1	7	5286.239
2	$S_{(.)}G''=G'_{(.)}\ pi_{(ct)}p_{(.)}c_{(.)}$	5237.3411	1.9206	0.22272	0.3828	8	5286.136
3	$S_{(.)}G''_{(.)}G'_{(.)}\ pi_{(ct)}p_{(.)}c_{(.)}$	5237.7049	2.2844	0.18568	0.3191	9	5284.473
4	$S_{(.)}G''_{(t)}G'_{(t)}\ pi_{(ct)}p_{(.)}c_{(.)}$	5243.789	8.3685	0.00886	0.0152	14	5280.376
5	$S_{(t)}G''_{(t)}G'_{(t)}\ pi_{(ct)}p_{(.)}c_{(.)}$	5248.5411	13.1206	0.00082	0.0014	18	5276.929
6	$S_{(t)}G''_{(t)}G'_{(t}\ pi_{(t)}p_{(.)}c_{(.)}$	5253.671	18.2505	0.00006	0.0001	22	5273.81
7	$S_{(.)}G''=G'_{(.)}\ pi_{(.)}p=c_{(.)}$	5343.7837	108.3632	0	0	5	5398.641
8	$S_{(t)}G''=G'_{(.)}\ pi_{(.)}p=c_{(.)}$	5347.7415	112.321	0	0	9	5394.509
9	$S_{(.)}G''=G'_{(t)}\ pi_{(.)}p=c_{(.)}$	5348.6568	113.2363	0	0	8	5397.451
10	$S_{(.)}G''_{(t)}G'_{(t)}\ pi_{(.)}p=c_{(.)}$	5350.9022	115.4817	0	0	11	5393.607
11	$S_{(t)}G''=G'_{(t)}\ pi_{(.)}p=c_{(.)}$	5353.0891	117.6686	0	0	12	5393.758
12	$S_{(t)}G''_{(t)}G'_{(t)}\ pi_{(.)}p=c_{(.)}$	5354.6408	119.2203	0	0	15	5389.183
13	$S_{(1)}G''=G'_{(0)}\ pi_{(.)}p=c_{(.)}$	5563.7925	328.372	0	0	3	5622.677

S- Survival; G''-Temporary emigration; G'- Probability of staying away ; pi- probability of mixture; p- capture probability; c- recapture probability; ct-time period indicating low and high camera trap density, hence t=2, t- primary periods/years; $G''_{(0)}$ Temporary emigration fixed at zero and $G'_{(1)}$- Probability of staying away fixed at 1 which means Temporary immigration (1-G') is zero

Table S.2: Model selection statistics for robust design analysis of Block II tiger capture data from Corbett National Park, India, 2010–2015.

Sno	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
1	$S_{(.)}G''_{(0)}G'_{(1)}pi_{(ct)}p_{(.)}c_{(.)}$	4479.2869	0	0.54437	1	7	4582.088
2	$S_{(.)}G''_{(.)}G'_{(.)}\ pi_{(ct)}p_{(.)}c_{(.)}$	4481.3182	2.0313	0.19715	0.3622	8	4582.088
3	$S_{(.)}G''=G'_{(.)}\ pi_{(ct)}p_{(.)}c_{(.)}$	4481.3182	2.0313	0.19715	0.3622	8	4582.088
4	$S_{(.)}G''=G'_{(t)}\ pi_{(ct)}p_{(.)}c_{(.)}$	4484.1023	4.8154	0.04901	0.09	11	4578.755
5	$S_{(.)}G''_{(t)}G'_{(t)}\ pi_{(ct)}p_{(.)}c_{(.)}$	4486.9908	7.7039	0.01156	0.0212	14	4575.49
6	$S_{(t)}G''_{(t)}G'_{(t)}\ pi_{(t)}p_{(.)}c_{(.)}$	4493.3215	14.0346	0.00049	0.0009	22	4565.232
7	$S_{(t)}G''_{(t)}G'_{(t)}\ pi_{(ct)}p_{(.)}c_{(.)}$	4494.5714	15.2845	0.00026	0.0005	18	4574.809
8	$S_{(.)}G''=G'_{(t)}\ pi_{(.)}p=c_{(.)}$	4550.8279	71.541	0	0	8	4651.598
9	$S_{(.)}G''_{(t)}G'_{(t)}pi_{(.)}p=c_{(.)}$	4551.7581	72.4712	0	0	11	4646.411
10	$S_{(t)}G''_{(t)}G'_{(t)}\ pi_{(.)}p=c_{(.)}$	4559.2726	79.9857	0	0	15	4645.712

S- Survival; G''-Temporary emigration; G'- Probability of staying away ; pi- probability of mixture; p- capture probability; c- recapture probability; ct-time period indicating low and high camera trap density, hence t=2, t- primary periods/years; $G''_{(0)}$ Temporary emigration fixed at zero and $G'_{(1)}$- Probability of staying away fixed at 1 which means Temporary immigration (1-G') is zero

Table S.3: Model selection statistics for robust design analysis of combined dataset of tiger capture from Corbett National Park, India, 2010–2015.

Sno	**Model**	**AICc**	**Delta AICc**	**AICc Weights**	**Model Likelihood**	**Num. Par**	**Deviance**
1	$S_{(.)}G''_{(0)}G'_{(1)}\ pi_{(ct)}p_{(.)}c_{(.)}$	9436.141	0	0.54321	1	7	9941.936
2	$S_{(.)}G''=G'_{(.)}pi_{(ct)}p_{(.)}c_{(.)}$	9438.155	2.014	0.19844	0.3653	8	9941.936
3	$S_{(.)}G''_{(.)}G'\ pi_{(ct)}p_{(.)}c_{(.)}$	9438.446	2.305	0.17157	0.3158	9	9940.212
4	$S_{(.)}G''=G'_{(.)}pi_{(t)}\ p_{(.)}c_{(.)}$	9441.354	5.213	0.04008	0.0738	12	9937.062
5	$S_{(.)}G''_{(.)}G'_{(.)}pi_{(t)}\ p_{(.)}c_{(.)}$	9441.52	5.3796	0.03688	0.0679	13	9935.205
6	$S_{(.)}G''=G'_{(t)}\ pi_{(t)}\ p_{(.)}c_{(.)}$	9445.971	9.8301	0.00398	0.0073	15	9935.605
7	$S_{(t)}G''=G'_{(.)}pi_{(t)}\ p_{(.)}c_{(.)}$	9446.842	10.7016	0.00258	0.0047	16	9934.448
8	$S_{(t)}G''_{(.)}G'_{(.)}pi_{(t)}\ p_{(.)}c_{(.)}$	9447.349	11.2081	0.002	0.0037	17	9932.925
9	$S_{(.)}G''_{(t)}G'_{(t)}\ pi_{(t)}\ p_{(.)}c_{(.)}$	9449.573	13.4323	0.00066	0.0012	18	9933.117
10	$S_{(t)}G''=G'_{(t)}\ pi_{(t)}\ p_{(.)}c_{(.)}$	9450.831	14.6906	0.00035	0.0006	19	9932.342
11	$S_{(t)}G''_{(t)}G'_{(t)}pi_{(t)}\ p_{(.)}c_{(.)}$	9451.609	15.4678	0.00024	0.0004	19	9933.119
12	$S_{(t)}G''_{(t)}G'_{(t)}pi_{(ct)}p_{(.)}c_{(.)}$	9457.59	21.449	0.00001	0	18	9941.134
13	$S_{(.)}G''=G'_{(.)}pi_{(.)}p_{(.)}c_{(.)}$	9483.474	47.3333	0	0	7	9989.27
14	$S_{(t)}G''_{(t)}G'_{(t)}pi_{(.)}p_{(.)}c_{(.)}$	9488.561	52.4199	0	0	17	9974.137
15	$S_{(.)}G''_{(.)}G'_{(.)}pi_{(ct)}p=c_{(.)}$	9583.796	147.6555	0	0	7	10089.59
16	$S_{(t)}G''_{(t)}G'_{(t)}pi_{(t)}p=c_{(.)}$	9588.93	152.7894	0	0	20	10068.41
17	$S_{(t)}G''_{(t)}G'_{(t)}pi_{(ct)}p=c_{(.)}$	9598.473	162.3319	0	0	16	10086.08
18	$S_{(t)}G''_{(t)}G'_{(t)}pi_{(.)}p=c_{(.)}$	9620.089	183.9481	0	0	15	10109.72
19	$S_{(.)}G''=G'_{(.)}pi_{(t)}p_{(.)}c_{(.)}$	9671.387	235.2462	0	0	11	10169.12
20	$S_{(.)}G''_{(0)}\ G'_{(0)}\ pi_{(t)}p_{(.)}c_{(.)}$	9706.788	270.6469	0	0	10	10206.54

S- Survival; G''-Temporary emigration; G'- Probability of staying away ; pi- probability of mixture; p- capture probability; c- recapture probability; ct-time period indicating low and high camera trap density, hence t=2, t- primary periods/years; $G''_{(0)}$ Temporary emigration fixed at zero and $G'_{(1)}$- Probability of staying away fixed at 1 which means Temporary immigration (1-G') is zero

Table S.4: Estimated Survival (S), Movement (G'' & G'), probability of mixture (pi), capture(c) and recapture (p) probability and year-wise abundance estimates (N_{year}) from the best model(S(.)G"(0)G'(1)pi(t=2)p(.)c(.)) in Block I of the study area, Corbett National Park, 2010-2015

Sno.	Parameter	Estimate	SE
1	S	0.65	0.03
2	Gamma"	0	0
3	Gamma'	1	0
4	pi (low camera trap density time period)	0.22	0.04
5	pi (high camera trap density time period)	0.5	0.08
6	p (high detectable grp)	0.27	0.03
7	p (low detectable grp)	0.07	0.01
8	c (high detectable grp)	0.52	0.02
9	c (low detectable grp)	0.14	0.02
10	N_{2010}	56	5.46
11	N_{2011}	54	5.28
12	N_{2012}	63	5.9
13	N_{2013}	50	5
14	N_{2014}	70	3.89
15	N_{2015}	72	3.97

Table S.5: Estimated Survival (S), Movement (G'' & G'), probability of mixture (pi), capture(c) and recapture (p) probability and year-wise abundance estimates (N_{year}) from the best model (S(.)G"(0)G'(1)pi(t=2)p(.)c(.)) in Block II of the study area, Corbett National Park, 2010-2015

Sno.	**Parameter**	**Estimate**	**SE**
1	S	0.61	0.03
2	Gamma"	0	0
3	Gamma'	1	0
4	pi (low camera trap density time period	0.24	0.04
5	pi (high camera trap density time period)	0.63	0.06
6	p (high detectable grp)	0.3	0.03
7	p (low detectable grp)	0.08	0.01
8	c (high detectable grp)	0.55	0.02
9	c (low detectable grp)	0.16	0.02
10	N_{2010}	66	6.65
11	N_{2011}	60	6.25
12	N_{2012}	42	4.9
13	N_{2013}	61	6.35
14	N_{2014}	60	4.7
15	N_{2015}	69	5.14

Table S.6: Estimated Survival (S), Movement (G'' & G'), probability of mixture (pi), capture(c) and recapture (p) probability and year-wise abundance estimates (N_{year}) from the model (S(.)G"(0)G'(1)pi(t=2)p(.)c(.)) for the combined dataset, Corbett National Park, 2010-2015

Sno.	Parameter	Estimate	SE
1	S	0.64	0.02
2	Gamma"	0	0
3	Gamma'	1	0
4	pi (low camera trap density time period)	0.23	0.03
5	pi (high camera trap density time period)	0.55	0.05
6	p (high detectable group)	0.28	0.02
7	p (low detectable group)	0.07	0.01
8	c (high detectable group)	0.54	0.01
9	c (low detectable group)	0.15	0.01
10	N_{2010}	124	8.92
11	N_{2011}	117	8.57
12	N_{2012}	109	8.15
13	N_{2013}	109	8.15
14	N_{2014}	124	6.25
15	N_{2015}	139	6.74

Table S.7: Estimated abundance in block I (N I) and block II (N II), total abundance from block wise analysis (N I + N II) along with standard error estimated using Delta Variance method and abundance from analysis of the combined dataset (Combined N), Corbett National Park, 2010-2015

Year	N I	SE	N II	SE	N I + N II	SE	Combined N	SE
2010	55	5.46	65.7	6.65	120.7	8.55	124	8.92
2011	54.21	5.28	60.11	6.25	114.32	8.14	117	8.57
2012	63.24	5.9	41.93	4.9	105.17	7.86	109	8.15
2013	50.5	5	61.51	6.35	112.01	8.01	109	8.15
2014	69.9	3.58	60.26	4.7	130.16	6.07	124	6.25
2015	72.17	3.97	68.86	5.14	141.03	6.53	139	6.74

Table S.8: Yearwise model selection for spatially explicit density analysis in R platform, Corbett National Park, 2010-2015

Year	model	npar	logLik	AICc	dAICc	AICcwt
2010	D~1 g0~1 sigma~h2 pmix~h2	5	-1002	2014.636	0	0.7539
2010	D~1 g0~h2 sigma~h2 pmix~h2	6	-1001	2016.875	2.239	0.2461
2010	D~1 g0~h2 sigma~1 pmix~h2	5	-1021	2053.665	39.029	0
2010	D~1 g0~1 sigma~1 pmix~h2	4	-1036	2082.357	67.721	0
2012	D~1 g0~h2 sigma~h2 pmix~h2	6	-1425	2864.703	0	1
2012	D~1 g0~1 sigma~h2 pmix~h2	5	-1464	2940.672	75.969	0
2012	D~1 g0~h2 sigma~1 pmix~h2	5	-1661	3333.056	468.353	0
2012	D~1 g0~1 sigma~1 pmix~h2	4	-1708	3426.064	561.361	0
2013	D~1 g0~h2 sigma~h2 pmix~h2	6	-1263	2540.202	0	1
2013	D~1 g0~1 sigma~h2 pmix~h2	5	-1277	2566.226	26.024	0
2013	D~1 g0~h2 sigma~1 pmix~h2	5	-1329	2669.984	129.782	0
2013	D~1 g0~1 sigma~1 pmix~h2	4	-1335	2678.723	138.521	0
2014	D~1 g0~h2 sigma~h2 pmix~h2	6	-4021	8055.674	0	1
2014	D~1 g0~1 sigma~h2 pmix~h2	5	-4173	8357.065	301.391	0
2014	D~1 g0~h2 sigma~1 pmix~h2	5	-4253	8517.975	462.301	0
2014	D~1 g0~1 sigma~1 pmix~h2	4	-4284	8576.367	520.693	0
2015	D~1 g0~h2 sigma~h2 pmix~h2	6	-3507	7027.148	0	1
2015	D~1 g0~1 sigma~h2 pmix~h2	5	-3649	7308.958	281.81	0
2015	D~1 g0~h2 sigma~1 pmix~h2	5	-4070	8151.523	1124.375	0
2015	D~1 g0~1 sigma~1 pmix~h2	4	-4088	8185.904	1158.756	0

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RESEARCH ARTICLE

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Demography of a high-density tiger population and its implications for tiger recovery

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Abstract

1. Prioritizing conservation of source populations within landscapes is proposed as a strategy for recovering tigers globally. We studied population dynamics of tigers in Corbett National Park (CNP) in Indian *Terai*, which harbours the largest and highest density tiger population in any protected area of the world. Through population viability models, we demonstrate the importance of CNP in tiger recovery within western *Terai*.
2. We camera trapped 521 km^2 of CNP using open population capture–mark–recapture framework between 2010 and 2015 to estimate annual abundance, spatially explicit density, survival, recruitment, temporary movements, sex ratio and proportion of females breeding. We model metapopulation persistence with and without Corbett as a source within western *Terai* landscape at different levels of poaching and habitat connectivity.
3. In 6 years, we recorded 6,202 photo-captures of 307 individual tigers. Annual tiger abundance and density were stable at 120 (*SE* 19) and 14 (*SE* 3) per 100 km^2 respectively. Detection probability of tigers was 0.18 (*SE* 0.03) and detection-corrected male:female sex ratio was female biased (0.80 *SE* 0.13). Apparent annual survival probability was 0.79 (*SE* 0.05) for females and 0.60 (*SE* 0.04) for males. Survival of tigers in CNP (0.68 *SE* 0.12) was lower than that reported for other populations. CNP tigers showed high reproduction with 54.8 (*SE* 5.1)% females breeding and with addition of 35 (*SE* 8)% as new recruits to the population each year. Small tiger populations in western *Terai* with moderate poaching could only persist through dispersal from CNP.
4. *Synthesis and applications*. Corbett tiger population was characterized by a stable high density, high reproductive rate and low survival, resulting in high turnover rates (32%–48%) between successive years. Such source populations could sustain low-level poaching and with habitat connectivity, recover tiger populations across the landscape. This study establishes potential thresholds that can likely be achieved by tiger populations under optimal natural conditions and highlights the importance of prioritizing conservation of source populations within tiger landscapes. This information can be used to plan and implement realistic tiger recovery programmes globally.

KEYWORDS
breeding tigresses, Corbett National Park, population dynamics, PVA, recruitment, source population, survival, *Terai* Arc

1 | INTRODUCTION

Tigers (*Panthera tigris*), the flagship species of Asian forested ecosystems, have lost over 40% of their range in the last two decades primarily due to demand-driven poaching, loss of habitat and its prey (Dinerstein et al., 2007). In densely populated Asia, space allocation for tiger conservation is one of the most limiting factors. The situation becomes even more challenging since protected areas (PA) by themselves are often too small to sustain viable tiger population in the long term (Wikramanayake et al., 1998). The average size of a PA in India, which is home to about 70% of the world's wild tigers (Jhala, Qureshi, & Gopal, 2015), is 393 km^2 (http://www.wiienvis.nic.in/Database/ProtectedArea854.aspx). However, due to high prey densities, some of these PAs have the potential to support high tiger density and if they lie embedded in a contiguous forested landscape, they can help maintain viable tiger population in that landscape. Therefore, tiger conservation strategy in India aims to preserve such small areas within larger connected landscapes as metapopulations (Qureshi et al., 2014). High-density tiger population in core areas of tiger reserves is achieved by making them free of human settlement and their impacts through incentivized voluntary relocation (Wildlife Protection Act, 1972; amendment 2005 http://www.indiaenvironmentportal.org.in/files/THE-20WILD-20LIFE.pdf) and habitat management for enhancing prey density. These activities require high investments, and the National Tiger Conservation Authority spent 7–20 million USD annually on incentivized voluntary human resettlement from within core areas of Tiger Reserves between 2010 and 2015 (https://projecttiger.nic.in/content/144_6_VillageRelocation11thPlan.aspx and https://projecttiger.nic.in/content/148_6_VillageRelocation12thPlan.aspx). This strategy is in consonance with Walston et al. (2010) who recommended protecting source tiger populations as a priority since these areas encompass only 6% of the current tiger distribution but harbour nearly 70% of wild tigers. This tenet has been debated widely with opponents proposing that landscape scale conservation should be the priority for a wide-ranging carnivore like the tiger (Wikramanayake et al., 2011). Metapopulation models parameterized with realistic tiger demographic data that evaluate tiger population persistence at landscape scales along with real-life data on tiger recovery would help resolve this debate.

Information on tiger vital rates is sparse and pioneering work of Sunquist (1981) and Smith (1993) that used radiotelemetry on tigers in Nepal *Terai* still remains the best source of information on the subject. Subsequently, Kenny, Smith, Starfield, and McDougal (1995), Kerley et al. (2003), Karanth, Nichols, Kumar, and Hines (2006), Duangchantrasiri et al. (2016), Majumder, Qureshi, Sankar, and Kumar (2017) and Sadhu et al. (2017) used camera trap-based capture–mark–recapture (CMR) and known fate models to estimate survival and movement parameters of tigers. Studying wildlife demography through telemetry provides information on survival, dispersal and helps tease apart temporary movement from permanent ones. However, such studies are constrained by the number of animals that can be radio-tagged due to the limitation of resources and permission for capture. Alternatively, camera trap-based CMR has proved to be a useful approach to study vital rates of large carnivore populations (Duangchantrasiri et al., 2016; Harmsen et al., 2017; Karanth et al., 2006; Majumder et al., 2017; Sharma et al., 2014). Although camera trap-based CMR approach addresses the limited sample size of telemetry studies, the vital rates obtained by CMR cannot distinguish between mortality and permanent emigration (Pollock, 1982). However, information generated by well-designed camera trap study is useful in understanding many aspects of demography that include vital rates such as apparent survival, recruitment, movement, time-specific detection-corrected sex ratio and percentage of breeding females in the population. Recent approach using spatially explicit open capture (SECR) CMR models has attempted to distinguish between emigration and mortality (Ergon & Gardner, 2014; Gardner, Sollmann, Kumar, Jathanna, & Karanth, 2018). However, these approaches are still under development (Efford, 2019) and require a very large-scale camera trapping to capture dispersal events of large carnivores, making them impractical for application (Ergon & Gardner, 2014).

The *Terai* landscape is renowned for its productivity, high concentration of ungulates and therefore, ability to sustain some of the highest density of tigers in the world (Dinerstein, 1980; Sunquist, 1981; Smith, 1993). Long-term work on tigers in the Nepal *Terai* has provided information on tiger demography through telemetry (Smith, 1987, 1993; Sunquist, 1981) and camera trapping (Barlow et al., 2009). Most of our knowledge on population dynamics and vital rates of tigers in India is from central India (Majumder et al., 2017; Panwar, 1979; Sadhu et al., 2017; Schaller, 1967) and from the Western Ghats (Karanth et al., 2006). While Corbett on the Indian side of *Terai* harbours the single largest tiger population in a single protected area in the world, estimated at 169–261 tigers, with a density of 16 ± 1.60 tigers per 100 km^2 (Bisht et al., 2015; Contractor, 2007), this population remains data deficient in our understanding of tiger demography and ecology. Corbett provides a unique opportunity to study a system that has been able to sustain one of the highest tiger densities in the world. The mechanisms behind this are of importance in current times of limited space and vanishing large mammals. The demographic parameter estimates from a high-density tiger population at/or approaching carrying capacity can be used for model-based predictions (Karanth & Stith, 1999) so as to gain an understanding of long-term population dynamics as well as form a basis for management interventions. This information will also help set realistic targets for achievable tiger numbers, enabling work towards reaching the set objective of 'TX2 commitment' by Tiger range countries (https://www.wwf.de/fileadmin/fm-wwf/Publikationen-PDF/Global-Tiger-Recovery-Program-Nov-4.pdf, Global Tiger Initiative, Global tiger recovery program 2010–2022).

We sampled Corbett National Park (CNP) from 2010 to 2015 using camera trap-based open CMR framework. Apart from abundance, we estimate sex-specific survival rates, sex ratio, reproductive and turnover rates in this high-density tiger population. We subsequently use these parameters to model the metapopulation of tigers in western *Terai* and evaluate the importance of the source value of Corbett tiger population in sustaining long-term tiger persistence within the landscape. We compare our model results with observed recovery of tigers in the western *Terai* Landscape (Jhala, Qureshi, & Gopal, 2008; Jhala, Qureshi, Gopal, & Sinha, 2011; Jhala et al., 2015).

Most tiger populations are plagued with low density, low reproductive rates and high mortality rates. Tigers of Corbett are a contradiction of sorts, as they occur at high density with a reasonably large population and have high reproductive rates. Our study provides insights in the demographic processes that operate in high-density populations like Corbett. It spells hope for tiger conservation efforts and shows that establishing source tiger populations similar to that of Corbett within each tiger landscape is the first step towards global tiger recovery.

2 | MATERIALS AND METHODS

2.1 | Study area

Terai Arc Landscape in India can be divided into two parts, Western *Terai* between the Yamuna and Sharda rivers and Eastern *Terai*, the area east of the Sharda river (Harihar & Pandav, 2012). The study was conducted in 521 km^2 of CNP situated in the Western *Terai* (Figure 1), comprising the foothills of the Himalayas, the Shivalik range and the *doon* valley. Corbett Tiger Reserve forms the major source population of tigers in Western *Terai*, while Chitwan National Park in Nepal is the major source in Eastern *Terai*. Most striking feature of this landscape is the perennial water streams called *sots* that act as water sources for wildlife throughout the year. The rich alluvial system and perennial water source support a thriving ungulate population (64 [*SE* 8.6] Chital [*Axis axis*] per km^2 and 9 [*SE* 1.1] Sambar

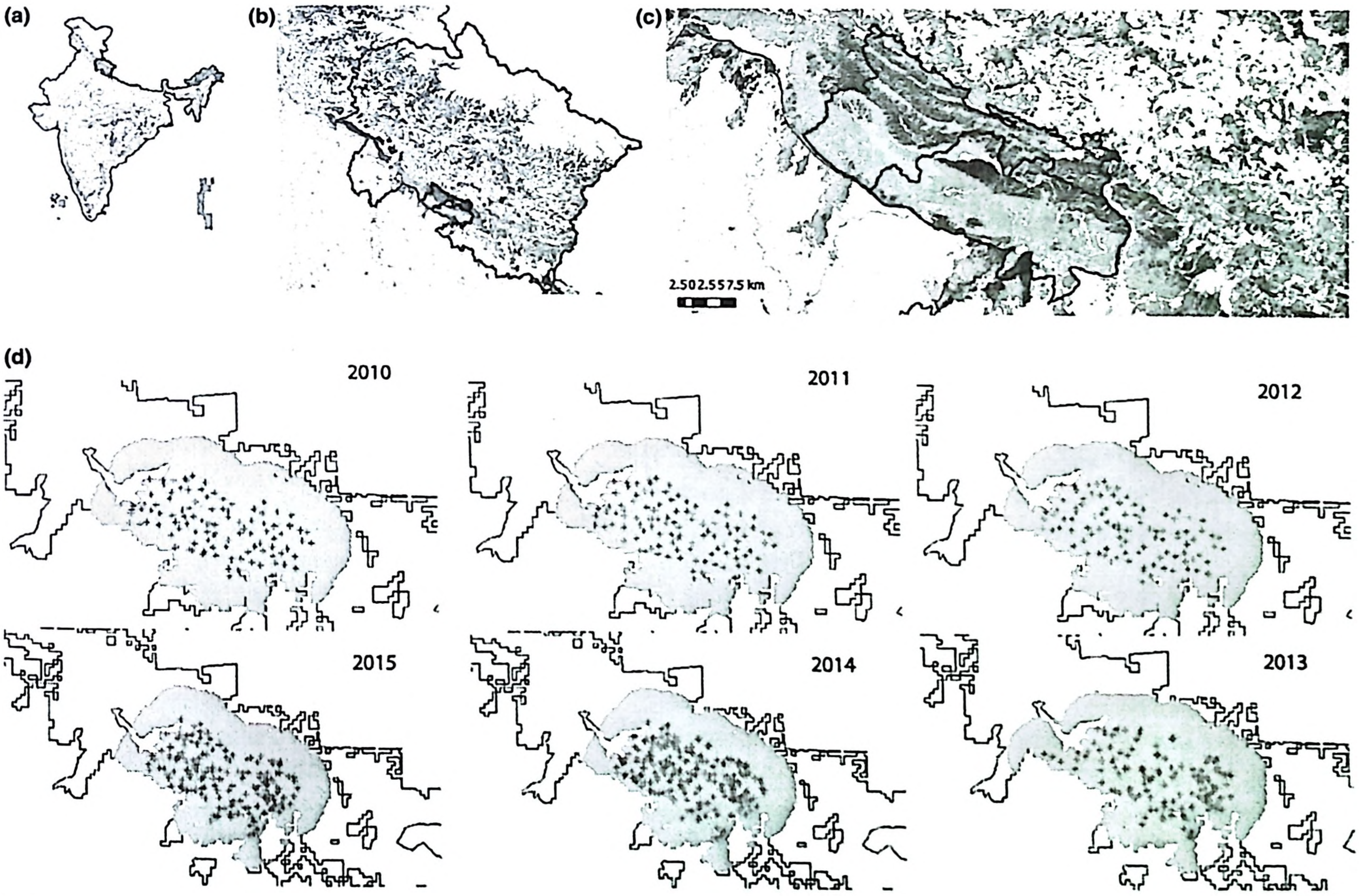

FIGURE 1 Map showing position of study area (Corbett National Park) overlaid on forest cover (green colour) map in (a) India and (b) state of Uttarakhand, (c) Corbett Tiger Reserve and (d) Camera trap locations (+) with a buffer of 8 km overlaid on tiger habitat mask for years 2010–2015 (clockwise)

TABLE 1 Tiger density (per 100 km^2) and major prey density (per km^2) from some important tiger conservation sites in India

Sites	Tiger	*SE*	Chital	*SE*	Sambar	*SE*	Source
Kanha	6.1	0.7	30.1	4.34	15.34	3.34	Awasthi et al. (2016), Kumar et al. (2015)
Ranthambhore	6.4	1	33.8	6.52	25.67	4.56	Sadhu et al. (2015)
Sunderbans	5.8	1.2	5.24	1.23	NA	NA	Roy et al. (2016)
Pench (Maharashtra)	3	0.6	15.69	7.14	6.6	2.9	Bhagat, Reddy, Joshi, Pariwakam, and Bansod (2015)
Rajaji	2.9	0.9	16.2	5.79	12.06	3.75	Pandav et al. (2015)
Nagarhole	11	0.9	29.85	4.36	3.56	0.57	Karanth, Kumar, Parameshwaran, Srivastha, and Sharma (2015)
Corbett	14	3	64	8.6	9	1.1	Bisht et al. (2015)

[*Rusa unicolor*] per km^2, Jhala et al., 2015) in the park as compared to some of the other Tiger Reserves in the country (Table 1).

Champion and Seth (1968) classified forests of CNP into three major types, namely Northern moist deciduous (3C), Northern tropical dry deciduous (5B) and Himalayan subtropical pine forest (9). Other than the Tiger, the park supports felids like Leopard *Panthera pardus*, Leopard cat *Prionailurus bengalensis* and Jungle cat *Felis chaus*. Other carnivores include Golden jackal *Canis aureus*, Sloth bear *Melursus ursinus*, Himalayan black bear *Ursus thibetanus*, Yellow-throated Marten *Martes flavigula*, Indian grey mongoose *Herpestes edwardsii*, Palm civet *Paradoxurus hermaphroditus*, Large Indian civet *Viverra zibetha*, Small Indian civet *Viverricula indica* and Smooth-coated otter *Lutrogale perspicillata*. Herbivores include Elephants *Elephas maximus*, Sambar, Chital, Barking deer *Muntiacus vaginalis*, Wild pig *Sus scrofa*, Hog deer *Axis porcinus*, Nilgai *Boselaphus tragocamelus*, Serow *Capricornis thar* and Goral *Naemorhedus goral*. The avifauna of CNP is also very rich with 554 species of resident and migratory birds of which 21 species are globally threatened (https://avibase.bsc-eoc.org).

2.2 | Data collection

We used CMR in a robust design framework (Pollock, 1982) by camera trapping 521 km^2 area of CNP consistently between 2010 and 2015. We deployed camera trap units that function on activity and passive infrared triggering mechanism to photograph tigers. Camera traps were deployed in pairs at each station, on either side of trails, so as to photo-capture both flanks simultaneously of each passing animal (Karanth & Nichols, 1998). Distance between camera trap stations was maintained between 1 and 1.5 km so as to ensure no 'holes' in the sampled area. This high camera density (Figure 1) ensured that all tigers in the study area had a good chance of photo-capture with no tiger having zero probability of photo-capture (Pollock, Nichols, Brownie, & Hines, 1990). Camera trap stations were selected based on reconnaissance sign surveys as well as expert knowledge of local field assistants. Potential camera trap point locations were recorded on the ground using a handheld GPS (Etrex 30 and Garmin 72); these locations were then plotted on Google Earth to select points for camera deployment to adhere to above-mentioned camera distance and correct for any sampling holes.

Due to logistic constraints (limited number of camera traps and field biologists) during the initial years (2010–2012), we sampled the study area in two blocks of ~250 km^2 area each. These two blocks were sampled 120–150 days apart. With increased availability of camera traps and trained field staff, we camera trapped the entire study area (521 km^2) simultaneously in 2013–2015 (see Table S1).

2.3 | Data analysis

Photographic captures and subsequent identification of tiger individuals through program EXTRACTCOMPARE (Hiby et al., 2009) yielded capture histories of individuals in the standard X-matrix format (Otis, Burnham, White, & Anderson, 1978). All CMR analyses excluded cubs (<1 year old) because of their low photo-capture probability and high mortality (Karanth et al., 2006). We grouped remaining >1-year-old tigers into a single age class because of difficulty in differentiating between adults and subadults from camera trap photos alone (Sadhu et al., 2017). Owing to a large sample size (n = 307) and ability to sex most individuals, we were able to obtain gender-specific parameter estimates.

2.4 | Population dynamics

We analysed capture data under the Robust design initially proposed by Pollock (1982) and subsequently modified by Kendall, Pollock, and Brownie (1995), Kendall, Nichols, and Hines (1997). Pollock's (1982) robust design was a two-stage analysis where abundance was estimated using closed population models for each primary period, while transition parameters were estimated between primary periods. All analyses were done in program MARK 8.x version 2017 (White & Burnham, 1999). Our study consisted of 6 years (2010–2015) of data with each year as a 'primary period' (Kendall et al., 1995, 1997; Pollock, 1982; Williams, Nichols, & Conroy, 2002). The tiger population was expected to be open to gains and losses between these primary periods while closed within the duration of sampling (42 days secondary periods) within each year. Kendall et al. (1995, 1997) developed a full likelihood approach that combined

Pollock's (1982) two step analysis into a single analysis. The full likelihood approach allows an animal to be unavailable for capture at any given time (or a temporary emigrant). The probability of availability is modelled to be (a) completely random or depends on whether the animal was (b) available for capture in the previous primary period or (c) actually captured in the previous primary period (Kendall et al., 1997). We first modelled capture probability (*detection models*) and subsequently, conditioning on the best selected detection model, we modelled state and transition parameters of interest (i.e. abundance, survival and movement) that were in consonance with tiger ecology.

Each of our primary period consisted of 42 camera trap nights (secondary periods). Between 2010 and 2012, sampling was carried out in two blocks (see Table S1). Between 2012 and 2013, due to the shift from two block sampling to a single block, tigers from the second block were exposed to an interval of 6 months between primary periods instead of 12 months. We explicitly account for this single shorter primary period by estimating separate survival rate for this 6-month period in MARK (Cooch & White, 2011) and subsequently converting it to annual survival for estimating average survival across years. By merging the blocks for analysis, we could likely violate the population closure assumption required for abundance estimation. Tigers are long-lived in comparison to our sampling interval (Mazak, 1981). We therefore tested if model selection and abundance estimates differed when (a) the two blocks were analysed separately (see Table S2a,b) and (b) data from the two blocks were merged for a single analysis (see Table S2c–f). Total population abundance for each year for this block analysis was estimated using a more parsimonious model (see Table S2c) in MARK that did not account for sex-based heterogeneity in detection and considered transition parameters to be constant. This approach was preferred for estimating total population size as a simpler model provided better precision on total abundance estimates. Since results from separate analyses of the two blocks and the combined analysis yielded abundance estimates that were not different from each other (see Table S2f,g), we subsequently report results from the combined dataset analyses as this increased sample size allowed us to estimate gender-specific parameters.

2.5 | Detection models

Here, we model individual detection probability based on the frequency of recaptures within a primary period, using maximum likelihood approach. We modelled individual detection probability (capture probability (p) and recapture (c)) by addressing the following sources of variability:

1. We hypothesized that the detection of tigers was likely to differ between sexes since territory size and movement rates differ between male and female tigers (Smith, 1993; Sunquist, 1981) and as also observed in jaguars (Sollmann et al., 2011). We modelled this potential source of variability in capture probabilities by incorporating sex as a covariate in the detection model.
2. Camera trap density was relatively low at 1 per 5 km^2 for the years 2010–2012 compared to a relatively high camera trap density of 2 per 5 km^2 for 2013–2015. We expect that detection probability of tigers would be higher during years (2013–2015) with higher camera trap density. We, therefore, modelled detection with two time period effects; period (a) 2010–2012 with low camera trap density and period (b) 2013–2015 with high camera trap density.

The full detection model (P) was $(P \sim p_{(m(ct), f(ct), u(ct))}; c_{(m(ct), f(ct), u(ct))})$ where capture (p) and recapture (c) were different for male (m), female (f) and unsexed tigers (u) for the two time periods (ct) that differed in camera density.

By accounting for heterogeneity caused by gender, effect of camera trap density along with traditional behaviour response ($p \neq c$) (Otis et al., 1978; Williams et al., 2002), we address the specific conditions in our study that could potentially account for variation in detection probability of tigers. Even though we had a 'large' sample (n = 307) of photo-captured tigers, this sample size was too small for more complex detection models like heterogeneity within gender groups, as these models did not converge.

2.6 | State and transition models

We modelled transition parameters such as survival and temporary movement rates using maximum likelihood approach on detection/non-detection of individuals across primary periods after accounting for detection probability within a primary period. Hence, using the best detection model(s), we subsequently model the state and transition. For these parameters, we evaluate the following hypotheses:

2.7 | Survival

There was no reason to suggest that habitat, prey or poaching differed in CTR between study years that could affect survival rates. Hence, we did not expect survival rates to differ between years. However, males and females have differential life-history traits (Smith, 1993) and should have different survival probabilities. We expected males to have lower survival compared to females as observed in most mammalian species (Krebs, 1972). We therefore modelled survival as constant (null model $S_{(.)}$) or differing between sexes ($S_{(g)}$).

2.8 | Movement

We did not expect movement parameters to change between years for the same reason as mentioned above. Males are the dispersing sex in tigers while females are more philopatric (Smith, 1993; Sunquist, 1981); we therefore expected movement in and out of the study area to differ between sexes. Corbett has one of the highest tiger densities in the world (Bisht et al., 2015; Contractor, 2007) and therefore competition for resources (food and mates) would also likely be high. If we found movement estimates to be very small (e.g. <0.1%) for either gender, we considered them to be negligible, and in our subsequent models, we fixed them at zero for parsimony and ease of computation.

Two movement parameters (Kendall et al., 1997), that is, temporary emigration (G″) and temporary immigration (1-G′) as defined below, were modelled.

1. Temporary emigration (G″) is the probability of going out of study area in a primary period if the animal was present in the previous primary period but remaining within the super population, and
2. Probability of staying away (G′) from the study area in a primary period given that the animal was part of the super-population in the previous primary period.

We fitted 16 models for the entire robust design analysis. We used sample size-corrected Akiake's information criteria (AIC_c) (Akaike, 2011) to select models which best explained our data from candidate competing models. To account for uncertainty associated with model selection, we used model averaging by AIC_c weights to average model parameters (Akaike, 2011).

2.9 | Abundance and spatially explicit density

The open CMR models (mentioned above) provide estimates of annual abundance ($\hat{N}$) as derived parameters in program MARK 8.x (White & Burnham, 1999). Density ($\hat{D}$) was estimated through likelihood-based spatially explicit capture recapture of tigers (Borchers & Efford, 2008; Efford, 2004) using package *secr ver.* 3.0.1 (Efford, 2017) in program R *ver* 3.4.1 (R Core Team, 2013). In SECR, we tested models where spatial scale of detection (σ) and capture probability of activity centres (g_0) were gender specific or similar between sexes.

2.10 | Sex ratio and reproductive rate

We estimated detection-corrected number of males and females from our best model to arrive at sex ratio. We examined each photo-capture event of females and termed them as 'breeding' if they were pregnant or lactating (Sadhu et al., 2017). Full udders and prominent nipples in a breeding female are visible about 7–10 days before parturition and till the cubs are weaned by 165 days (Gittleman, 1986; Smith & McDougal, 1991). From our long-term ad libitum observations in the study area, we found that one of the female's lactation period lasted for 155 days, which was similar to the lactation period mentioned in Gittleman (1986) and Smith and McDougal (1991). We sampled the study area for 42 days in a year; therefore, all females that delivered cubs ≤5 months before our sampling period would comprise the pool of breeding females available for sampling each year.

We estimated the actual number of breeding females (B_f) during the primary sampling by correcting the number of breeding females photo-captured by the detection probability of breeding females. $B_f = n_L/p_{bf}$, where n_L = number of breeding females detected in each primary sampling period, p_{bf} = probability of detecting a breeding female.

Since birth seasonality is not profound in tigers (Sunquist, 1981), we consider tigers to breed throughout the year for our computation. Breeding females (B_{fy}) in a year would be:

$$B_{fy} = B_f \times (\text{Days in a year} \div \text{Sampling Days}) \times (\text{Days Detected as Breeding} \div \text{Sampling Days})$$

$$B_{fy} = B_f \times (365 \div 42) \times (165 \div 42)$$

Since we could potentially have 8.69 intervals of 42-day sampling in a year and pregnancy/lactation was detectable for 165 days, a single breeding female could potentially be detected in 3.93 sampling intervals in 1 year.

2.11 | Recruitment and population trend

Recruitment is the number of new individuals added to the population in time *t* per individual at time *t* − 1. Recruitment in case of a camera trap study is the product of fecundity and survival from cub to >1-year-old tigers as well as immigrants from neighbouring areas. We estimated number of recruits (B_t) in time *t* as;

$$B_t = \hat{N}_{t+1} - \hat{N}_t \times S$$

where $\hat{N}_{t+1}$ = abundance estimate at time *t* + 1, $\hat{N}_t$ = abundance estimate at time *t*, *S* = survival probability (Skalski, Kristin, & Millspaugh, 2010).

Another important parameter for population dynamics is the population trend. We regressed natural log of tiger density against years (2010–2015). The slope of the regression provides an estimate of the instantaneous growth rate (*r*) (Caughley, 1977; Skalski et al., 2010). A significant positive slope implies an increasing population and a negative slope implies population decline, while a slope of zero implies a stationary population (Caughley, 1977). For a population near its carrying capacity, we expect the growth rate not to be significantly different from zero. With high potential for reproduction in tigers (Mazak, 1981), we hypothesize that, at carrying capacity, the recruits from CNP would disperse into the larger landscape so as to maintain a stationary population (growth rate near zero).

2.12 | Metapopulation viability analysis

In early 2006, the western *Terai* tiger population consisted of separate populations constituted by (a) Rajaji NP, (b) Corbett tiger reserve, (c) Ramnagar forest division and (d) Nandhore forest division. These populations though distinct, probably exchanged individuals occasionally through forested corridors constituted by the Shivalik hill forests and some remnant forests in valley habitats. Distances between these populations ranged between 1 and 146 km with varying magnitude of resistance to tiger movement in the intervening corridor habitats. Corbett NP harboured the largest tiger population numbering close to 108 ± 4.5 (Contractor, 2007). We evaluate the importance and role of Corbett tigers in sustaining and promoting tiger occupancy and abundance within the Western *Terai* landscape by modelling a Population Viability Analysis in Vortex ver. 9.9 (Lacy, 1993) using published tiger demography and parameters estimated by us in Corbett (Kenny et al., 1995; Sadhu et al., 2017; Smith, 1987, 1993; Smith & McDougal, 1991). We varied cub survival in our models to be between 0.65 and 0.55 to capture observed empirical estimates (Smith & McDougal, 1991) as well as reduced survival rates of juveniles and subadults to capture the lower limits of population persistence. We modelled realistic scenarios (see Table S3) wherein we evaluate persistence of single isolated populations of varied sizes (20, 50 and 100 tigers) exposed to various levels of poaching and catastrophic events. Subsequently, we model a metapopulation depicting the western *Terai* scenario with four populations and their initial tiger numbers as estimated in 2006 (initiation of the country-wide tiger estimation, Jhala et al., 2008). We model the metapopulation with Corbett population being small ~20 tigers and with its observed population size (≥200) to understand its role in sustaining long-term tiger persistence within the landscape. We also model a scenario wherein the landscape was depleted of tiger populations with only the source (Corbett) remaining. These scenarios address the specific case of prioritizing source population at the cost of smaller populations, answering whether such a strategy would permit long-term tiger persistence in the landscape. Movement rates between the four populations were based on our field observations from camera trap data (Jhala et al., 2008, 2011, 2015) and reducing these to half, so as to depict a higher resistance to movement in the landscape (loss of corridors). With the above models we test, Walston et al.'s 6% solution hypothesis wherein the authors propose to prioritize conserving source population within landscapes. We elucidate our model results by comparing them with observed increase in tiger occupancy and abundance within western *Terai* landscape.

3 | RESULTS

A total sampling effort of 35,784 camera trap-nights yielded 6,202 photographic captures of 307 individual tigers during our 6-year study (2010–2015) (Table 2). Of the 307 individuals, 130 were females, 118 males and 59 individuals whose gender could not be ascertained. Individuals in the unidentified gender group had 1–2 captures in a given primary period and were not photo-captured in succeeding years. Across all years, males on an average were photo-captured 11 (*SE* 1.2 range 1–72; median 6) times, while females had average photo-captures of 11.6 (*SE* 1.1 range 1–62; median 7).

3.1 | Open-CMR-robust design-based vital rates of tigers

3.1.1 | Detection probability

Tiger detection probability was best explained by the model that accounted for (a) gender-based differences (b) behavioural response of tigers and (c) the camera density. The closest competing model differed by a Delta AIC_c of 2.64 (Table 3). Detection probability for all years was high at 0.86 (*SE* 0.04) for all tigers with no difference between males (0.86, *SE* 0.01) and females (0.87, *SE* 0.01). The overall capture probability was 0.8 (*SE* 0.04) during years with low camera trap density and 0.92 (*SE* 0.05) for high-density camera trap years.

Using the best detection model, the state and transition model that had the lowest AIC_c (Table 3) accounted for gender differences in survival had no temporary movement for males and unidentified gender class while accounting for random temporary movements in females. Model estimates of survival and movement parameters differed between males (0.6 *SE* 0.04) and females (0.79 *SE* 0.05) with females having higher survival and temporary movements (Table 4).

3.1.2 | Abundance, density and recruitment

Tiger numbers ranged from 109 to 139 over the 6 years of study (Table 5). Estimates of detection probability (g_0) at the activity centre for males (0.08 *SE* 0.02) and females (0.12 *SE* 0.05) were similar. While the spatial scale of detection, σ, which is a measure of activity range radius for males (2.11 *SE* 0.24 km), was almost

TABLE 2 Details of sampling effort, detections and number of individual tigers photo-captured within 521 km^2 of consistently camera trapped area of Corbett National Park, 2010–2015

Primary period	CT density	Trap-nights	No. photo-captures	M_{t+1}	Cumulative no. of tigers	#M	#F	No. breeding females
2010	Low	4,326	466	89	89	36	43	11
2011		4,410	461	98	129	34	37	10
2012		4,410	925	93	162	30	33	8
2013	High	6,300	1,183	109	201	31	39	8
2014		9,324	1,135	118	251	34	62	7
2015		7,014	2,032	115	307	50	62	16

Abbreviations: CT density, Camera trap density; Low, one per 5 km^2; High, two per 5 km^2; M_{t+1}, unique individuals photo-captured; #M, Number of male tigers; #F, Number of female tigers.

TABLE 3 Model selection statistics for detection and transition models using the robust design analysis on tiger photo-capture data from Corbett National Park, 2010–2015

S. no	Model	AIC$_c$	Delta AIC$_c$	AIC$_c$ weights	Model Likelihood	Num. par	Deviance
Detection models							
1	$S_{(.)}G'_{(.)}G''_{(.)}\,p_{(M(ct),\,F(ct),\,U(.))}c_{(M(ct),\,F(ct),\,U(.))}$	17,408.82	0.00	0.82	1.00	14	17,217.96
2	$S_{(.)}G'_{(.)}G''_{(.)}p_{(g,ct)}c_{(g,ct)}$	17,412.53	3.71	0.13	0.16	16	17,217.63
3	$S_{(.)}G'_{(.)}G''_{(.)}p_{(g)}c_{(g)}$	17,521.81	112.98	0.00	0.00	9	17,341.03
4	$S_{(.)}G'_{(.)}G''_{(.)}p_{(ct)}c_{(ct)}$	17,743.04	334.22	0.00	0.00	7	17,566.29
5	$S_{(.)}G'_{(.)}G''_{(.)}p_{(.)}c_{(.)}$	17,898.81	489.99	0.00	0.00	5	17,726.07
6	$S_{(.)}G'_{(.)}G''_{(.)}p{=}c_{(g)}$	17,917.80	508.98	0.00	0.00	6	17,743.06
7	$S_{(.)}G'_{(.)}G''_{(.)}p{=}c_{(t)}$	18,148.45	739.63	0.00	0.00	5	17,975.72
8	$S_{(.)}G'_{(.)}G''_{(.)}p{=}c_{(.)}$	18,306.76	897.94	0.00	0.00	4	18,136.03
Transition models							
1	$S_{(g)}G'_{(F,M=U=0)}G''_{(F,M=U=0)}p_{(M(ct).\,F(ct).\,U(.))}c_{(M(ct).\,F(ct).\,U(.))}$	17,404.70	0.00	0.60	1.00	17	17,207.77
2	$S_{(g)}G'_{(.)}G''_{(.)}\,p_{(M(ct),\,F(ct),\,U(.))}c_{(M(ct).\,F(ct),\,U(.))}$	17,407.34	2.64	0.16	0.27	17	17,210.41
3	$S_{(g)}G'{=}G''_{(.)}\,p_{(M(t),\,F(ct),\,U(.))}c_{(M(ct),\,F(ct).\,U(.))}$	17,408.41	3.71	0.09	0.16	16	17,213.50
4	$S_{(.)}G'_{(.)}G''_{(.)}\,p_{(M(ct),\,F(ct),\,U(.))}c_{(M(ct),\,F(ct),\,U(.))}$	17,408.82	4.13	0.08	0.13	14	17,217.96
5	$S_{(.)}G'{=}G''_{(.)}\,p_{(M(ct).\,F(ct),\,U(.))}c_{(M(ct),\,F(ct).\,U(.))}$	17,410.14	5.44	0.04	0.07	13	17,221.30
6	$S_{(.)}G'{=}G''_{(g)}\,p_{(M(ct),\,F(ct),\,U(.))}c_{(M(ct),\,F(ct),\,U(.))}$	17,411.06	6.37	0.02	0.04	14	17,220.20
7	$S_{(g)}G'_{(g)}G''_{(g)}p_{(g,ct)}c_{(g,ct)}$	17,414.18	9.48	0.01	0.01	22	17,207.11

Abbreviations: S, survival; G'', temporary emigration; G', probability of staying away; p, capture probability; c, recapture probability; g, gender; M, males; F, females; U, unidentified gender; ct, are the two time periods differing in camera trap density; (.), parameter kept constant.

TABLE 4 Model averaged estimates of capture (p),recapture (c) probability, survival (S) and temporary movement (G''& G') for female and male tigers in Corbett National Park, 2010–2015

Gender	Camera trap density	Detection parameters	Estimate (*SE*)	Survival (*SE*)	Gamma' (*SE*)	Gamma'' (*SE*)
Female (*n* = 130)	Low	p	0.05 (0.007)	0.79 (0.05)	0.58 (0.24)	0.22 (0.06)
		c	0.12 (0.005)			
	High	p	0.07 (0.007)			
		c	0.18 (0.005)			
Male (*n* = 118)	Low	p	0.06 (0.007)	0.60 (0.04)	0	0
		c	0.14 (0.006)			
	High	p	0.06 (0.007)			
		c	0.20 (0.007)			

Abbreviations: G'', temporary emigration; G', probability of staying away.

double than that of females (1.1 *SE* 0.75 km). Overall tiger density was stable at 14 (*SE* 3) per 100 km^2 from 2010 to 2015 (Table 5). Detection-corrected sex ratio (male:female) was 0.80 (*SE* 0.13, Table 5).

3.1.3 | Reproductive rate

During each sampling period, 32%–39% of photo-captured females were found to be breeding (Table 2) and the proportion of females actually breeding was estimated to be 54.8 (*SE* 5.1)%, amounting to an average of 28 (*SE* 3.2) females breeding each year within the study area.

3.1.4 | Population trend

The slope (*r*) of the regression of ln (D) versus years was not different from zero ($r = 0.003 \pm 0.03$, $p = 0.93$, $R^2 = 0.002$) suggestive of a stationary tiger population (Figure 2).

3.1.5 | Metapopulation viability

Small tiger populations <20 were liable to go extinct by themselves in the next 100 years (Table 7); such populations were extremely sensitive to poaching with extinction probability increasing to almost 100% even with one tiger being poached annually (Table 7). Medium

TABLE 5 Abundance, spatially explicit density, sex ratio, movement parameter (σ) and detection probability (g_o) at activity centres of tigers in Corbett National Park, 2010–2015

Abundance estimates from MARK					Density estimates from SECR					
Yr	$\hat{N}_F$ (SE)	$\hat{N}_M$ (SE)	$\hat{N}$ (SE)	M:F	ESA (km^2)	$\hat{D}$ (SE)	σ F (SE) (km)	σ M (SE) (km)	g_0 F (SE)	g_0 M (SE)
2010	50 (4.10)	43 (3.39)	124 (8.92)	0.84	586	16 (1.6)	1.43 (0.06)	2.12 (0.09)	0.03 (0)	0.03 (0.003)
2011	43 (3.67)	40 (3.37)	117 (8.57)	0.92	601	14 (1.6)	1.06 (0.03)	2.01 (0.08)	0.12 (0.01)	0.05 (0.004)
2012	39 (3.38)	36 (3.01)	109 (8.15)	0.91	635	14 (1.6)	0.8 (0.02)	2 (0.05)	0.05 (0)	0.2 (0.002)
2013	46 (3.81)	37 (3.08)	109 (8.15)	0.79	590	12 (1.2)	1.3 (0.05)	2.56 (0.1)	0.01 (0)	0.08 (0.009)
2014	68 (3.22)	37 (2.36)	124 (6.25)	0.55	735	17 (1.5)	1.04 (0.7)	1.8 (0.6)	0.3 (0.02)	0.09 (0.006)
2015	68 (3.22)	56 (3.03)	139 (6.74)	0.81	790	15 (1.4)	1 (0.07)	2.18 (0.02)	0.2 (0)	0.04 (0.003)

Abbreviations: $\hat{N}_F$, population estimate of females; $\hat{N}_M$, population estimate of males; $\hat{N}$, overall population estimate (including unsexed tigers); M:F, detection corrected male to female ratio; $\hat{D}$, spatially explicit density; σ, sigma, the movement parameter; g_0, detection probability; ESA, effective sampling area; Yr, year.

(>50) to large populations (>100) had high persistence probability and large populations could also buffer low levels of poaching-related mortality (2M and 1F annually). The simulated landscape of western *Terai* had very high persistence for the next 100 years in the absence of poaching and could also accommodate moderate tiger offtake/poaching from each of the four populations before the survival of the metapopulation was at risk (Table 7). However, in the absence of Corbett as a source population thereby reducing immigration, individual populations showed extinctions (Table 7, Scenario 16 &17).

In the scenarios when all tiger populations (except Corbett) were extirpated, dispersal from Corbett re-established these populations in the landscape. Reducing permeability of corridors connecting these populations by half impacted recolonization and increased extinction risks (Table 7, Scenario 13).

4 | DISCUSSION

Tiger density (12–17 per 100 km^2) within CNP is one of the highest recorded in the world and leads to a quiver of questions about how large carnivore populations might behave when crowded to this extent. In the first ever long-term monitoring of tigers in the Indian *Terai*, we attempt to characterize this population and provide useful and novel insights into this important source population. This study constitutes one of the largest camera trap dataset obtained for any large carnivore in the world, enabling us to model complex combinations of parameters (Gerber, Ivan, & Burnham, 2014) and for the first time estimate gender-specific survival and other vital parameters for tigers.

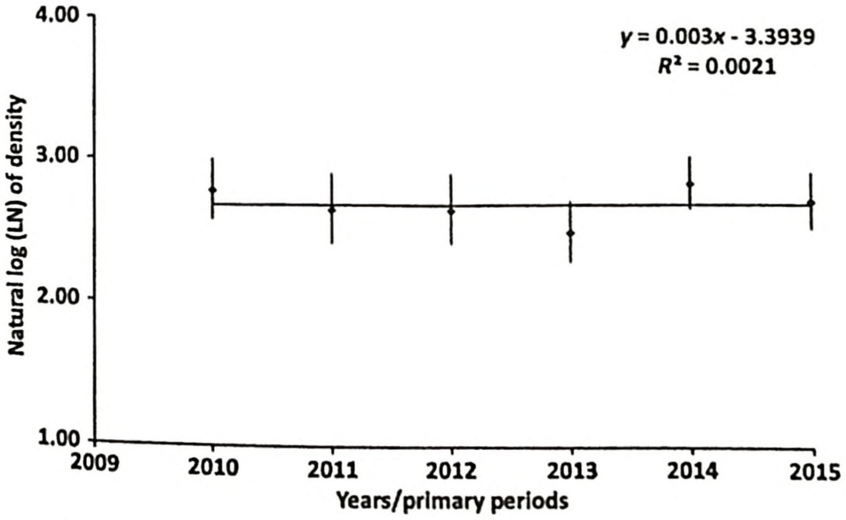

FIGURE 2 Natural log of tiger density (with 95% confidence intervals) plotted against years for 2010–2015 in Corbett National Park

For the robust design, population closure is a prerequisite for abundance estimation within secondary periods, while the population is open between primary periods for estimates of survival and movement parameters. Therefore, our block approach in sampling (2010–2012) could adversely affect population estimates due to violation of population closure assumption within the primary periods but would not have any influence on other parameter estimates like survival which were addressed with appropriate analysis. However, independent and pooled estimates of abundance of the blocks did not differ (see Table S2g). Since both adjacent blocks had high tiger density, movement between them was restricted, and we found only 4–5 individual tigers common between the two adjacent blocks (amounting to 4% of the population). Therefore, combining the data of the two blocks for the first 3 years did not alter our inferences on annual population abundances.

4.1 | Detection probability

Larger movement of males, that is, larger home range leads to a greater σ in SECR compared to females. Tigers in our study had high capture probabilities. Increase in camera trap density resulted in increased capture probability by 12%, mainly due to better detection of the proportion of the population that inherently had low detectability (unsexed tigers). While for sexed individuals (males and females), the capture probability increased by about 4%.

4.2 | Survival

Survival estimated in CMR studies is apparent survival which includes death and permanent emigration. Survival probability

TABLE 6 Comparative review of camera trap-based open capture–mark–recapture studies carried out on tigers from across their range

Parameters	Nagarhole[a]	Huai Kha Khaeng[b]	Pench[c]	Corbett[d]
Survival	0.77 (*SE* 0.05)	0.80–0.96	0.66 (*SE* 0.04)	0.68 (*SE* 0.02)
Temporary emigration	0.10 (*SE* 0.07)	Not reported	Not reported	0.2 (*SE* 0.08)[e]
Mean maximum distance moved (km)	3.74 (*SE* 0.56)	4.37 (*SE* 1.05)	5.33 (*SE* 0.91)	4.6 (*SE* 0.96)M 2.8 (*SE* 0.77)F
Density/100 km^2	9.7 (*SE* 1.8)	1.68 (*SE* 0.69)	3.70 (*SE* 0.8)	14 (*SE* 3.0)
Growth rate (%)	3 (*SE* 0.2)	5 (*SE* 0.3)	15 (*SE* 0.11)	0.3 (*SE* 3.0)

Note: Mean Maximum Distance Moved-For all individual tigers with recaptures the maximum distance between camera traps with captures was recorded and averaged. For Corbett, we have separate estimates for males (M) and females (F).

[a] Karanth and Sunquist (1995), Karanth et al. (2006), Karanth and Sunquist (2000).

[b] Duangchantrasiri et al. (2016).

[c] Majumder et al. (2017).

[d] Current study.

[e] Temporary emigration estimate for the females, males in the study did not show temporary movements.

varied between genders, where apparent annual survival probability of males (0.60) was much lower than that of females (0.79). Of 130 females photo-captured during the study period (2010–2015), we identified 61 (~50%) to be residents since they were photo-captured in two or more primary periods compared to 38% males who were residents. Females are philopatric and this is reflected in their survival rates, while low survival rate of males is characteristic of large carnivores, which are exposed to higher risks and are the dispersing gender in tigers (Smith, 1993). None of the published studies on population dynamics of tigers from open CMR have estimated gender-specific survival because of relatively small datasets (Karanth et al., 2006, $n = 78$; Majumder et al., 2017, $n = 66$ and Duangchantrasiri et al., 2016, $n = 90$) (Table 6). Hence, lack of gender-specific estimates from India and across the tiger's range limits our comparison of estimates. The overall estimate of annual apparent survival of adult tigers (0.68) in Corbett was lower than that reported for tigers in South India (0.77, Karanth et al., 2006) and in Thailand (0.82, Duangchantrasiri et al., 2016). High density likely leads to intense competition which is reflected as depressed apparent survival rates. A telemetry study on Corbett tigers and/or large-scale (>2,000 km^2) long-term camera trapping (Ergon & Gardner, 2014) is required to further tease apart emigration from mortality as well as provide insights into dispersal and territoriality.

4.3 | Recruitment and source population

Corbett tiger population is a paradox of sorts as it maintains a stable high-density population yet has low apparent survival rates. With over 54.8 (*SE* 5.1)% females found breeding each year with a high level of recruitment (35 [*SE* 8]%), this likely results in high emigration and turnover rates in the population. The number of breeding females within CNP exceeds the number recommended for long-term viable tiger source populations (20–25, Chapron et al., 2008; Gopal, Sinha, Mathur, Jhala, & Qureshi, 2007 and PVA results Table 7). Tiger population in Nagarhole and Russian Far East were observed to increase at 3%–6% (Karanth, Nichols, Kumar, Link, & Hines, 2004 and Miquelle, Smirnov, Zaumyslova, Soutyrina, & Johnson, 2015). CNP tiger population remained stable across years. The population fluctuated between 109 and 139 tigers within the study area of ~500 km^2 and was likely to be at carrying capacity where recruitment replaces deaths and emigration. Considering the mortality rate of Corbett tigers to be similar to tigers in Ranthambhore (10%–16%, Sadhu et al., 2017) which was also at high density, the apparent mortality of 32% can then be partitioned into actual mortality (10%–16%) and 16%–22% to emigration. This suggests that 19–26 tigers disperse annually out of CNP, highlighting the importance of CNP as good source population (Pulliam, 1988) for the landscape.

4.4 | Movement

Competition renders temporary movements inefficient as individuals are unlikely to regain territories once lost. We found different temporary movement rates between females and males in Corbett. Males showed little to no temporary movement. This suggests that males either moved permanently out of the study area or died. This is in consonance with tiger ecology (Smith, 1993) where males are the dispersing sex and permanently disperse out of the natal area to minimize inbreeding (Pusey, 1987).

Industrial development, mining, palm plantations, highways and other linear structures are fragmenting prime wildlife habitat across Asia. Large carnivore conservation is limited by shrinking space as forested areas are converted into smaller islands. This problem is amplified in India which is a hub for development. Tiger occupancy within India's tiger landscapes is maintained by protecting at least one significant source population within each landscape. Our simulation results show the importance of a large source in a landscape, as also proposed by Walston et al. (2010). In the absence of such a source connected to other populations, tiger persistence within smaller populations in a landscape was prone to extinction events and could not tolerate even moderate offtake by poachers. Small isolated tiger populations were extremely vulnerable to extinction especially in the face of poaching as also shown by Chapron et al. (2008). Due to the current illegal demand for tiger body parts, it would practically be impossible to stop poaching entirely. Although efforts to minimize

TABLE 7 Single and metapopulation viability analysis results for the western Terai landscape from 17 scenarios (Table S3a–c) in Vortex 9.9. All the results are from models run with parameters reported in Table S3b and the models with reduced parameters are reported in Table S5

Scenario	PopName	N_0	K	Dispersal	Harvest	S-r (*SD*)	PE	*N*-ext (*SD*)	*N*-all (*SD*)	Me.TE
1	SmallPop	15	20	NA		0.04 (0.17)	0.24	16.4 (3.84)	12.48 (7.71)	54
2	MedPop	30	50	NA		0.05 (0.11)	0	45.22 (5.12)	45.09 (5.68)	65
3	MedPop	30	50	NA	1M+1F	−0.01 (0.15)	0.71	37.03 (11.18)	10.94 (17.95)	39
4	LargePop	75	100	NA		0.05 (0.09)	0	92.47 (7.91)	92.47 (7.91)	0
5	LargePop	75	100	NA	2M+1F	0.03 (0.09)	0	88.88 (8.69)	88.79 (9.13)	61
6	LargePop	75	100	NA	2M+2F	0.03 (0.11)	0.1	89.16 (9.91)	79.92 (28.71)	44
7	Rajaji	15	50	Normal		0.06 (0.13)	0	42.24 (7.45)	42.24 (7.45)	0
	Corbett	120	200			0.02 (0.08)	0	175.68 (15.89)	175.68 (15.89)	0
	Ramnagar	35	50			0.06 (0.13)	0	42.02 (7.72)	42.02 (7.72)	0
	Nandhore	10	30			0.08 (0.15)	0	25.24 (4.98)	25.19 (5.08)	43
	Metapop	180	330			0.04 (0.06)	0	285.12 (22.18)	285.12 (22.18)	0
8	Rajaji	15	50	Normal	1M	0.06 (0.15)	0.04	41.38 (9.13)	39.94 (11.47)	19
	Corbett	120	200		2M+1F	0.02 (0.08)	0.01	169.3 (18.12)	168.29 (22.31)	51
	Ramnagar	35	50		1M	0.06 (0.14)	0	41.89 (7.54)	41.82 (7.71)	68
	Nandhore	10	30		1M	0.06 (0.19)	0.11	22.53 (7.29)	20.61 (8.82)	23
	Metapop	180	330		5M+1F	0.03 (0.06)	0	270.66 (29.83)	270.66 (29.83)	0
9	Rajaji	15	50	Half		0.06 (0.13)	0	41.21 (7.69)	41.17 (7.79)	33
	Corbett	120	200			0.04 (0.07)	0	182.34 (14.26)	182.34 (14.26)	0
	Ramnagar	35	50			0.05 (0.13)	0	41.48 (7.71)	41.48 (7.71)	68
	Nandhore	10	30			0.06 (0.16)	0	24.26 (5.1)	24.21 (5.2)	46
	Metapop	180	330			0.04 (0.06)	0	289.19 (20.75)	289.19 (20.75)	0
10	Rajaji	15	50	Half	1M	0.05 (0.15)	0.22	39.57 (10.79)	31.17 (18.32)	17
	Corbett	120	200		2M+1F	0.03 (0.08)	0	178.34 (15.49)	178.34 (15.49)	0
	Ramnagar	35	50		1M	0.05 (0.14)	0	41.06 (8.4)	40.95 (8.64)	50
	Nandhore	10	30		1M	0.03 (0.22)	0.67	13.51 (10.2)	6.16 (8)	18
	Metapop	180	330		5M+1F	0.04 (0.06)	0	256.61 (27.5)	256.61 (27.5)	0
11	Rajaji	0	50	Normal		0.08 (0.15)	0	42.04 (7.79)	42.04 (7.79)	0
	Corbett	120	200			0.02 (0.08)	0	175.58 (16.13)	175.58 (16.13)	0
	Ramnagar	0	50			0.08 (0.15)	0	41.87 (7.54)	41.87 (7.54)	0
	Nandhore	0	30			0.09 (0.17)	0	25.56 (5.01)	25.56 (5.01)	0
	Metapop	120	330			0.04 (0.06)	0	285.05 (21.89)	285.05 (21.89)	0

(Continues)

TABLE 7 (Continued)

Scenario	PopName	N_0	K	Dispersal	Harvest	S-r (*SD*)	PE	*N*-ext (*SD*)	*N*-all (*SD*)	Me.TE
12	Rajaji	0	50	Normal	1M	0.049 (0.23)	0.32	27.9 (18.01)	20.17 (18.64)	0
	Corbett	120	200		2M+1F	0.02 (0.08)	0	169.66 (17.87)	168.98 (20.81)	43
	Ramnagar	0	50		1M	0.17 (0)	0.006	42.01 (7.89)	41.77 (8.44)	0
	Nandhore	0	30		1M	0.22 (0.22)	0.17	21.09 (8.46)	18.29 (9.95)	0
	Metapop	120	330		5M+1F	0.07 (0.004)	0.004	250.21 (30.43)	249.21 (34.23)	43
13	Rajaji	0	50	Half		0.07 (0.16)	0	41.39 (7.71)	41.39 (7.71)	0
	Corbett	120	200			0.04 (0.07)	0	181.81 (15.04)	181.81 (15.04)	0
	Ramnagar	0	50			0.07 (0.15)	0	41.19 (8.01)	41.19 (8.01)	0
	Nandhore	0	30			0.07 (0.18)	0	24.45 (5.32)	24.45 (5.32)	0
	Metapop	120	330			0.05 (0.06)	0	288.84 (21.41)	288.84 (21.41)	0
14	Rajaji	0	20	Half		0.05 (0.24)	0.84	9.71 (6.11)	1.87 (4.26)	0
	Corbett	20	30			0.03 (0.15)	0.1	24.27 (5.41)	21.85 (8.86)	60
	Ramnagar	0	20			0.05 (0.24)	0.57	10.2 (5.24)	4.7 (5.89)	0
	Nandhore	0	20			0.05 (0.23)	0.78	11 (6.41)	2.74 (5.36)	0
	Metapop	20	90			0.03 (0.13)	0.08	33.77 (11.35)	31.16 (14.14)	60
15	Rajaji	0	20	Reduced		0.06 (0.22)	0.95	24.69 (17.72)	1.51 (6.89)	0
	Corbett	20	30			0.04 (0.14)	0.06	25.06 (4.95)	23.6 (7.55)	59
	Ramnagar	0	20			0.06 (0.21)	0.78	25.68 (17.88)	5.85 (13.32)	0
	Nandhore	0	20			0.06 (0.23)	0.94	13.88 (10.29)	1.14 (4.28)	0
	Metapop	20	90			0.04 (0.14)	0.05	33.81 (17.17)	32.1 (18.3)	58
16	Rajaji	0	50	Half		0.13 (0.2)	0.51	41 (15.58)	20.25 (23.01)	0
	Corbett	20	30			0.10 (0.1)	0	28.47 (3.32)	28.47 (3.32)	0
	Ramnagar	0	50			0.12 (0.2)	0.12	43 (12.24)	38.02 (17.82)	0
	Nandhore	0	30			0.13 (0.2)	0.18	24.72 (7.91)	20.48 (11.62)	0
	Metapop	20	160			0.11 (0.13)	0	107.22 (34.22)	107.22 (34.22)	0
17	Rajaji	0	50	Reduced		0.04 (0.18)	0.24	16.09 (3.71)	12.23 (7.53)	49
	Corbett	20	30			0.04 (0.14)	0.03	25.48 (4.8)	24.77 (6.28)	62
	Ramnagar	0	50			0.03 (0.18)	0.18	14.57 (4.8)	12.09 (6.86)	56
	Nandhore	0	30			0.04 (0.18)	0.17	16.28 (3.98)	13.56 (7)	43
	Metapop	20	160			0.04 (0.09)	0	62.65 (15)	62.65 (15)	0

Abbreviations: S-r, Stochastic growth rate; PE, Probability of extinction; *N*, ext-Population size at year 100 for populations that did not go extinct; *N*-all, average population size for all the populations; M.TE, Median time for extinction; Me.TE, Mean time for extinction; M, adult male; F, adult female; PopName, Population name; LargePop, Large population ($n = 75$, K = 100); MedPop, Medium population ($n = 30$, K = 50); SmallPop, Small population ($n = 15$, K = 20); MetaPop, Metapopulation; N_0, Initial Population; K, Carrying capacity.

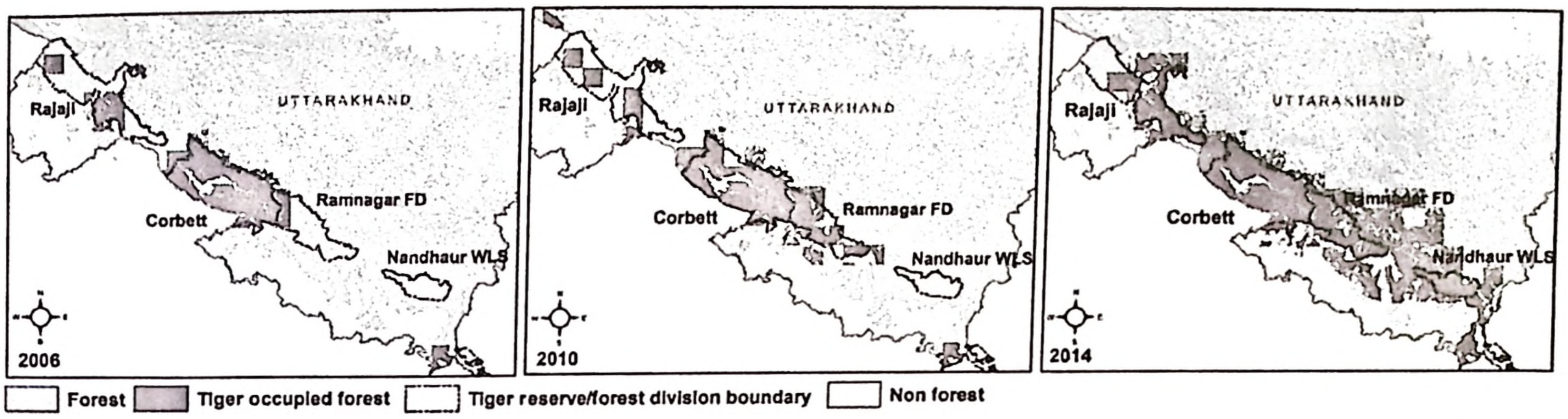

FIGURE 3 The *Terai* landscape was sampled for tiger signs by a 15 km search within each 15 km^2 forested patch as part of the occupancy survey for national tiger status evaluation (Jhala et al., 2008, 2011, 2015). Forest patches where tiger sign was detected are marked in brown. Expansion in tiger occupancy from Corbett Tiger Reserve across western *Terai* landscape is clearly seen from 2006 to 2014

poaching through patrolling and law enforcement are required, simultaneously, a strategy to increase recruitment by having a good source population (>100) in the landscape that buffers the offtake of poachers would ensure tiger persistence. The PVA results corroborate the prioritization of resource allocation to important source populations within landscapes (Walston et al., 2010) as without securing them first, tiger recovery within large landscapes is difficult. However, Walston et al. (2010) do not advocate conservation of only source populations but propose to prioritize them for allocating limited resources. Our results acknowledge the relevance of landscape scale conservation as tiger occupancy of the landscape can only be possible with functional dispersal corridors. Prior to 2006, tiger populations were estimated by unreliable means (Karanth et al., 2003) and the official tiger estimate for India was 3,642 tigers (Narain, Panwar, Gadgil, Thapar, & Singh, 2005). Subsequent to the local extinctions of Sariska and Panna tigers caused due to poaching in 2005 and 2009 (Check, 2006; Gopal, Qureshi, Bhardwaj, Singh, & Jhala, 2010), the first tiger status estimation based on modern scientific approach was implemented and put the population at a precariously low number of 1,411 (1,165–1,657; Jhala et al., 2008). At that time, camera trap study in CNP (2006–2007) estimated the population to be at 108 (*SE* 4.5) within the same area of 500 km^2 (Contractor, 2007) as the current study. This was identified as one of the few sources of tigers remaining within the country and was prioritized for conservation investment (Jhala et al., 2008). After 2006, investment in stringent protection and resettlement of human habitation were undertaken and over 300 families were rehabilitated from within the core area of Corbett TR under the new incentivized voluntary rehabilitation package (Narain et al., 2005; Wildlife Protection Act, 1972, 2006 amendment). By 2012, the entire Corbett Tiger Reserve (1,288 km^2) had a tiger density comparable to that of the CNP, with Corbett Tiger Reserve being home to about 143–198 tigers (Bisht et al., 2012). This strategy of high investment in a source population has paid dividends and resulted in an increase in tiger occupancy and numbers in the larger landscape of western *Terai* between 2006 and 2014 (Figure 3), where tigers have increased from 178 (*SE* 17) individuals occupying 1,901 km^2 to 340 (*SE* 41) individuals occupying 6,576 km^2 (Jhala et al., 2008, 2011, 2015).

The high-density source population of CNP was characterized by a stable population with high proportion of females breeding, high recruitment, low apparent survival and high turnover of individuals. These characteristics permitted tigers to be produced at rapid rates to disperse and populate most available habitat within the landscape within a period of 8 years. The optimal *Terai* and foothill habitats were almost all occupied by tigers by 2014, and tigers are now dispersing to high altitude habitats as well (Bhattacharya & Habib, 2016). Our study documents potential thresholds that can be achieved by tiger populations under optimal conditions. This information and the strategy of focusing conservation efforts on source populations within each landscape can be used to plan and implement realistic tiger recovery programmes globally.

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AUTHORS' CONTRIBUTIONS

Y.J. and Q.Q. conceived, designed and secured the resources for the study; Shikha and Sudip conducted the field work; Shikha and Y.J. analysed the data; Shikha and Y.J. wrote the manuscript. All authors contributed critically to the drafts and revisions and gave final approval for publication.

DATA ACCESSIBILITY

Data for the Robust design CMR is available via the Dryad Digital Repository https://doi.org/10.5061/dryad.vc3143h (Bisht, Banerjee, Qureshi, & Jhala, 2019). Details of PHVA parameterization are available in the Supporting Information. Tigers are susceptible to poaching; therefore, Spatial Data on tiger captures have not been archived.

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SUPPORTING INFORMATION

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