
**Understanding aspects of demography and resource partitioning
mechanisms of large felids along with abundance and spatial
distribution of prey in Similipal Tiger Reserve, Odisha**

A THESIS

Submitted by

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for the award of the Degree of

**DOCTOR OF PHILOSOPHY IN
WILDLIFE SCIENCE**

Under the supervision of

Dr. Bivash Pandav & Dr. Yadvendra V. Jhala



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JUNE 2024

Citation:

RATHORE H. S. (2024). Understanding aspects of demography and resource partitioning mechanisms of large felids along with abundance and spatial distribution of prey in Similipal Tiger Reserve, Odisha. Ph.D. Thesis. Wildlife Institute of India, Dehradun, India, and Saurashtra University, Rajkot, India. Pp- 1-152.



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Declaration by the Candidate

I hereby declare that the thesis entitled “*Understanding aspects of demography and resource partitioning mechanisms of large felids along with abundance and spatial distribution of prey in Similipal Tiger Reserve, Odisha*” is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Doctor of Philosophy in Wildlife Science** to the **Saurashtra University, Rajkot (Gujarat)**. This research work has been carried out under the guidance and supervision of **Dr. Bivash Pandav, Scientist-G**, and co-supervision of **Dr. Yadvendradev V. Jhala, Former Dean of Wildlife Institute of India, Dehradun**. The work has not formed the basis for the award of any other degree, diploma, associateship, fellowship, titles in this or any other university or other institution of higher learning. I also declare that the thesis embodies my own work, analysis, observation, understanding and the particulars given in it are true to the best of my knowledge.

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I certify that the research work was appreciated by all who were present, and the comments made by the faculty and researchers have been appropriately included in the thesis.

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01	Name of the Research Scholar	HARSHVARDHAN SINGH RATHORE
02	Title of the Thesis/Dissertation	“UNDERSTANDING ASPECTS OF DEMOGRAPHY AND RESOURCE PARTITIONING MECHANISMS OF LARGE FELIDS ALONG WITH ABUNDANCE AND SPATIAL DISTRIBUTION OF PREY IN SIMILIPAL TIGER RESERVE, ODISHA”
03	Name of the supervisor	Dr. BIVASH PANDAV
04	Department/Institution/Research Centre	WILDLIFE INSTITUTE OF INDIA, DEHRADUN
05	Similar Content (%) identified	3%
06	Acceptable Maximum Limit	10%
07	Software Used	iThenticate
08	Date of Verification	13.06.2024

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Acknowledgement

"In the end, we will conserve only what we love; we will love only what we understand; and we will understand only what we are taught." — Baba Dioum

This phrase sums up my life experiences and also teaches the value of direction and support in my life. I was inspired and felt solace in nature at an early age, and this led to a passion for wildlife conservation. However, without my parent's support and love, my enthusiasm would not have blossomed. Words alone hardly explain how much I appreciate you, but I would like to thank you from the bottom of my heart for all of your sacrifices, patience, and understanding. This accomplishment is both yours and mine.

Embarking on this PhD journey has been an experience filled with both triumphs and challenges. It has been happiness, discovery, failures, and thoughts of being sure or not. I have had the assistance, advice and support of many amazing people to whom I owe all the gratitude in the world. Therefore, I would like to thank the people who helped me to their best and collaborated for the excellent outcome of the study that made it an unforgettable experience.

To begin with, I offer my humble gratitude and warmest thanks to the Director, the Dean, and the former and present Research Coordinator at WII for giving me this opportunity. The institute facilitated a focused and productive atmosphere, enabling me to dedicate myself sincerely to a positive outcome. I also thank them for providing me with all the logistics & guidance to carry out the study.

I am deeply indebted to my supervisor Dr. Bivash Pandav for supporting me in every step of this journey and for providing just the right balance of independence and guidance. From my master's dissertation to my PhD research, you have been a constant source of inspiration and guidance. I always look up to you with the utmost respect and admiration. I am more than grateful for your kind encouragement, immensely valuable ideas, and guidance throughout this endeavour.

Taking this opportunity, I would like to extend my heartfelt gratitude to my co-supervisor Dr. Yadvendradev V. Jhala. Despite your demanding schedule and fatigue, your considerate availability to clarify doubts and offer positive reinforcement has been indispensable. Your insights have shaped my academic journey and your prudent advice will remain a lasting source of scientific learning throughout my life.

Though words are seldom enough to thank Dr. Samrat Mondol I am more than obliged for your invaluable guidance whether assisting me with scientific writing or instilling the importance of attention to detail and timely task completion. Your guidance has taught me the value of time management and precision benefits that I will reap for a long time. Thank you for your support and mentorship.

It is indeed a pleasing privilege to express my gratitude to Prof. Qamar Qureshi for encouraging the best in me and acknowledging my true potential so that I could come out of my comfort zone. Your constructive criticism, ability to put complex ideas into simple terms and every bit of assistance have got me to where I am today. You have been a constant confidant throughout these years. I am more than grateful.

I am cordially thankful to Dr. Vishnupriya Kolipakam & Dr. S.P. Goyal for assisting me in gaining focus when I was overtaken by ideas. Your thoughts clarity and

direction have not only helped me in the study but also will be of great help in the future.

My sincere thanks must also go to Shri. Suresh Chandra Mahapatra, IAS (Retd.), Chief Advisor to Chief Minister Office and ex-chief Secretary, Odisha for providing his valuable insights during the study. The discussions on the study during his visits to Similipal provided us with immense knowledge and encouragement.

I am very grateful to the Odisha Forest Department & National Tiger Conservation Authority for funding this work. I express my deep sense of gratitude to Shri. Debidutta Biswal, IFS, PCCF & HOFF, Odisha and Shri. Susanta Nanda, IFS, PCCF Nodal & PCCF (WL) & CWLW, Odisha for their unfailing support in the execution and completion of this work.

I would like to express our sincere gratitude to Dr. Manoj V. Nair, IFS, Director Nandankanan & CCF Wildlife, Odisha for providing me with all the kind help & valuable guidance during the study. His immense knowledge of big cats and vast experience of the Similipal landscape kept me on the right track from the beginning of the study.

I express our sincere thanks to Dr. Debabrata Swain, IFS (Retd.), Ex-PCCF & HOFF, Odisha, Dr. Sandeep Tripathi, IFS (Retd.), Ex-PCCF & HOFF, Odisha, Dr. Hari Shankar Upadhyay, IFS (Retd.), Ex- PCCF (WL) & CWLW, Odisha and Shri Shashi Paul, IFS (Retd.), Ex-PCCF (WL) & CWLW, Odisha for their kind support & guidance.

I am very grateful to Shri. Amitav Brahma, IFS (Retd.) and Shri. M. Yogajayanand, IFS, CEO, CAMPA & CCF (PP & A) for providing valuable guidance during their tenures as Field Director, Similipal Tiger Reserve.

I fell short of words in expressing our gratitude towards Dr. J.D. Pati, IFS, DFO Athagarh Forest Division & Wildlife Conservation Officer, Odisha and Dr Shyama Bharti, OFS, ACF, Dhenkanal Division. They had been the architect of the study & were involved in every aspect of the research, be it the ground-level implementation to rigorous scientific scrutiny. I owe my deepest gratitude to them for their unwavering supervision, support & encouragement throughout the process. The work would have been nearly impossible without their efforts.

My heartfelt thanks to Dr. Samrat Gouda, IFS, Deputy Director, Similipal Tiger Reserve for his constant support, guidance and encouragement throughout the project duration.

I'm extremely grateful to Shri. Sai Kiran D N, IFS, Deputy Director, Similipal Tiger Reserve for providing us with important inputs & crucial support to carry out the research. I greatly acknowledge all the help provided by Shri. Pradeep Kumar Dey, OFS, ACF, Similipal Tiger Reserve, Shri. Bidya Sagar, OFS, ACF, Angul Division & Shri. Samaresh Biswal, OFS, ACF, Similipal Tiger Reserve for on-field execution of the project activities.

I am very thankful to all the Range Officers of Similipal Tiger Reserve for providing us with the necessary facilities & help in the field to carry out the study. A special thanks to Mr. Saifuddin Malik & Mr. Pankaj Das for providing all the help when

required. I greatly acknowledge the support provided by the frontline staff of Similipal Tiger Reserve in the field as they had been the backbone of this study.

I am deeply saddened by the loss of fallen warriors, the Late Mathy Hansdah (Forester) and Late Bimal Jena (Forest Guard) in the line of duty. I salute their sacrifice. I had some of my best field experiences with them.

I also want to acknowledge and extend my thanks to field assistants Buddhram Naik and Laxman Dalei for their outstanding work and dedication. From long days in challenging conditions to meticulous data collection, your contribution has been invaluable.

I am also wholeheartedly thankful to Dr. Ujjwal Kumar and Dr. Neha Awasthi. From the very beginning and throughout every step of my journey, you have been a constant source of support and encouragement. Thank you for always being a listening ear, I am profoundly grateful and deeply indebted to your kindness and invaluable assistance. Dr. Ujjwal Kumar has always been my source of guidance in all the matters and immensely helped me in understanding complex topics in simple manner.

I cannot forget to mention my friends Prashant, Shrey, Medhavi Ma'am, Mariyam, Yogita, Rahul, Nirdesh, Rubal, Vikas and Dipak, thank you for boosting my morale from time to time for your incredible support during some of the most stressful times in my life helped me a lot.

I would also like to greatly acknowledge the help provided by Dr. Neeraj Mahar, Jayant Bhai, Ms. Rutu, Ms. Shravana, Mr. Ankit Pacha, Ms. Shreshree & Ms. Shiv Patel in this endeavour.

I would like to thank my juniors Omkar, Dhruv, Anil, Vaishanvi, Tarun, Lovepreet, Shalu and Swati who have always been a helping hand whenever I needed it.

I also want to extend my thanks to Ms. Kumudani Bala Gautam for helping me with my thesis submission in Saurashtra University.

Many people have shared their time with me generously and have contributed in various ways to my PhD studies; I owe my sincere thanks to Dr. C.P. Sharma, Shri. Gyanesh Chhiber, Shri. Rakesh Sundriyal, Shri. M. M. Uniyal and Sanjay Ji every single one of you has been a wonderful support throughout this journey.

Numerous others have quietly championed me from afar, and although not specifically named, each played an important role in my journey so I express my gratitude to all, whom I have forgotten to mention.

Last but not least, I also gratefully acknowledge the help of the various authors whose works have been quoted in this work which are mentioned herein. I am highly indebted to various national and international organizations and ministries for their data, statistics and reports available on official websites which made this study a successful one.

Finally, I would like to end this section with these beautiful words by the “Master”

“This planet has to be loved, this planet has to be rejoiced in. It is a gift.” — Osho

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List of Abbreviations:

AIC- Akaike Information Criterion

BRG- Brooks-Rubin-Gelman

CJS- Cormack-Jolly-Seber

CMR- Capture-Mark-Recapture

DIC- Deviance Information Criterion

Dist_vil- Distance to Villages

Dst_meadow- Distance to Meadow

DSM- Density Surface Modelling

ETA- Effective Trapping Area

FSI- Forest Survey of India

GAMs- Generalized Additive Models

GPS-Global positioning System

GTRP- Global Tiger Recovery Program

HDI- High Density Interval

HWS- Hadagarh Wildlife Sanctuary

IUCN- International Union of Conservation of Nature

JAGS- Just Another Gibbs Sampler

KWS- Kuldiha Wildlife Sanctuary

LWE- Left-Wing Extremists

MSTriPES- Monitoring System for Tigers: Intensive Protection and Ecological Status

MCMC- Markov Chain Monte Carlo

NDVI- Normalized Difference Vegetation Index

NTCA-National Tiger Conservation Authority

ROPE- Region of Practical Equivalence

SECR- Spatially Explicit Capture Recapture

STR- Similipal Tiger Reserve

WII- Wildlife Institute of India

WPSI- Wildlife Protection Society of India



CHAPTER- 1

Introduction

Background

Earth's biodiversity is severely threatened by the booming human population and its concomitant ramifications (White, 2000). *Species extinction* is the ultimate blow resulting from the chain of local extinction of the populations throughout their original distributional range (Gilpin & Soulé, 1986; Clark, 1990). Various studies have revealed that among threatened mammals, the large-bodied (i.e., >20 kg) are twice as likely to become extinct in general (Ceballos *et al.*, 2005; Schipper *et al.*, 2008); Karanth *et al.*, 2010). Large carnivores are mainly among the first to disappear from habitat degradation (Hunter, 1998). Despite being the world's most iconic and admired species, approximately 61% of large carnivores are in imminent danger and threatened, as per the International Union for Conservation of Nature (IUCN) (Ripple *et al.*, 2014). Anthropogenic factors like habitat loss and fragmentation, human persecution, and the decline in prey and utilisation of medicines and fur have been the primary causes of their reduction. Large energy requirements, slow life histories, existence at low population densities, the need for vast areas to forage for large prey make large carnivores susceptible to clashes with humans, which they barely cope with (Karanth & Chellam, 2009; Ripple *et al.*, 2014; Woodroffe & Ginsberg, 1998).

Carnivores of different sizes are essential in regulating ecosystems (Beschta & Ripple, 2009; Prugh *et al.*, 2009; Estes *et al.*, 2011; Ritchie *et al.*, 2012). The intensity and

strength of their impression rely on their size, density, metabolic needs, sociality, and hunting style (Cardillo *et al.*, 2004; Cardillo *et al.*, 2005; Carbone *et al.*, 1999). Large carnivores act as umbrella species in their respective habitats throughout the globe (Roberge & Angelstam, 2004). As keystone species in several ecological systems, top predators restrict large herbivore populations through predation and meso-carnivores through intra-guild competition, thereby having a top-down effect on ecosystems (Ripple & Beschta, 2006; Ripple & Beschta, 2007; Dalerum *et al.*, 2008; Owen-Smith & Mills, 2008; Ripple *et al.*, 2014). The eradication of predators disrupts the ecosystem balance and generates ripples that ultimately trickle down to the lowest rung of the trophic ladder (Morrison *et al.*, 2007; Ritchie *et al.*, 2009). Thus, large carnivore conservation is the key to preserving high levels of biodiversity (Terborgh *et al.*, 2010).

The reliable assessment of population parameters is essential for developing effective conservation strategies for large carnivores, ensuring their long-term survival within their natural habitat (Boitani & Powell, 2012). While research efforts in India have excelled in estimating tiger abundance at specific sites (Jhala *et al.*, 2019; Qureshi *et al.*, 2023), similar studies on vital rates (birth and death rates) of tigers remain scarce. Existing research on tiger vital rates is limited to only a few regions of the country, such as parts of western ghats, western India, Terai Arc Landscape and central Indian landscape (Karanth *et al.*, 2006; Sadhu *et al.*, 2017; Bisht *et al.*, 2019; Kumar *et al.*, 2019). However, the east-central landscape encompassing the Indian states of Jharkhand, Chhattisgarh and Odisha has witnessed a documented decline in tiger occupancy (Jhala *et al.*, 2021). This region also suffers from a significant research gap regarding multi-year large felid research. Similarly, reliable information on

demographic parameters in leopard populations remains scarce across India. A single study by Kumar (2019) in Kanha Tiger Reserve offers some insights; this lack of widespread data creates challenges for effective conservation efforts.

Prey abundance is also a major threat for the carnivore conservation. Studies have shown a positive correlation between the carnivore population and the abundance of prey (Fuller, 2001). Limited food resources, often a consequence of declining prey populations due to human activities (Woodroffe, 2000), can have a direct negative impact on predator abundance. This decline is further exacerbated by increased intraspecific competition for the remaining resources, as seen in studies on various large carnivores (Packer *et al.*, 2005; Watts & Holekamp, 2008). Notably, Carbone and Gittleman (2002) suggest a general rule: approximately 10,000 kg of prey is required to sustain 90 kg biomass of carnivore population, irrespective of the species. Moreover, limited prey availability has been linked to global tiger population declines across various regions (Karanth & Stith, 1999; Wolf & Ripple, 2016; Qureshi *et al.*, 2023). Despite extensive forest cover, this scarcity highlights the critical role of prey abundance and distribution in maintaining the tiger population (Jhala *et al.*, 2020).

Similipal Tiger Reserve (STR) in Odisha stands out as the largest breeding tiger population within the east-central Indian landscape (Rathore *et al.*, 2021). Furthermore, it holds significance as the only known habitat for wild pseudo-melanistic tigers (Jhala *et al.*, 2015; Sagar *et al.*, 2021 Qureshi *et al.*, 2023). This unique ecosystem also fosters the coexistence of sympatric leopard with tiger (Nayak, 2014; Palei *et al.*, 2015). However, critical information regarding the population dynamics and how these large carnivores coexist within the same area remains scarce

(Palei *et al.*, 2023). Thus, multi-year studies are urgently needed to address this knowledge gap and develop effective management plans to recover tiger and leopard populations. These studies should focus on various tiger and leopard demography aspects, including population trends, age-sex structure, survival and recruitment rates. Additionally, implementing robust assessments of prey populations and prioritizing their conservation efforts can contribute to the unintended benefit of tiger conservation, a concept known as 'collateral conservation' (Wolf & Ripple, 2016). Therefore, assessments of prey abundance and distribution within the landscape are crucial and research emphasizing coexistence strategies is fundamental. Prioritizing management efforts solely towards the tiger population growth could further impact the co-predators such as the leopard and may even lead to a decline in their populations (Kumar *et al.*, 2019). Hence, research focussed on coexistence is crucial for effectively managing tiger and leopard in this region.

Literature Review

Tiger and Leopard – Status and Distribution

Tiger

The tiger is the largest felid in the world, with three extinct and six extant subspecies (Hunter, 2015). Classified as globally endangered by the IUCN Red List of Threatened Species (Goodrich *et al.*, 2022), this apex predator has shown signs of recovery. For instance, the estimated wild tiger population increased from 3200 individuals in 2010 to around 5000 in 2023 (GTRP, 2023). Tigers exhibit remarkable ecological adaptability, thriving in diverse habitats, such as tropical, subtropical, temperate forests, forest-grassland mosaics, dense floodplain grasslands, thickets,

scrub, and marshes (Nowell & Jackson, 1996). However, the history of the tiger paints a bleaker picture. Their dominion once spanned vast areas of Asia, extending from eastern Turkey through central Asia and forming a continuous range from the Afghanistan-Pakistan border, encompassing South and Southeast Asia to Bali in the east and the Russian Far East (Hunter, 2015). This historical distribution highlights the significant range of contraction tigers have experienced in recent centuries. Since last 100 years, tigers have disappeared entirely from southwestern and central Asia, Bali and Java, and most of their range in Southeast and Eastern Asia (Goodrich *et al.*, 2022; Sanderson *et al.*, 2023). This translates to a current distribution limited to roughly 7-8% of their former range, with the remaining populations confined in isolated forest patches (Sanderson *et al.*, 2006; Walston *et al.*, 2010; Sanderson *et al.*, 2023).

Habitat fragmentation and degradation are the major threats to tiger conservation (Odden *et al.*, 2010; Seidensticker *et al.*, 2010; Gubbi *et al.*, 2016; Smith *et al.*, 2018). Additionally, poaching fuelled by the demand for body parts and high-value products, coupled with prey decline and human-wildlife conflict in recent decades, further compound the challenges for the tiger population globally (Smith *et al.*, 2018). Despite their endangered status, a significant gap exists in our understanding of wild tiger demography on a global scale. However, few other studies on wild tiger demography provide valuable data for joining the dots in tiger conservation (Smith & McDougal, 1991; Kerley *et al.*, 2003; Karanth *et al.*, 2006; Duangchantrasiri *et al.*, 2016).

Tigers hold iconic status in India (Jhala *et al.*, 2015). This charismatic species is protected under Schedule I of the Wildlife (Protection) Act, 1972. India is home to the world's largest wild tiger population, with an estimated 3682 ± 243 individuals in 2022 (Qureshi *et al.*, 2023). This represents a significant increase in the tiger population from 2967 (2603-3346) in 2018 (Jhala *et al.*, 2019), showing annual growth rate of 6.1% (Qureshi *et al.*, 2023). Even though India's tiger population constitutes approximately 75% of the global wild tigers (GTRP, 2023), the species still faces a multitude of threats.

Habitat loss and fragmentation, driven by infrastructure development, agriculture, human encroachment, continue to plague tigers across most of their range in India (Jhala *et al.*, 2015). This habitat destruction makes it harder to find prey and mate, apart from vast area requirements for territories and dispersal. Furthermore, the lack of well-connected corridors between these fragmented habitats further restricts movement and gene flow, potentially leading to isolated and vulnerable subpopulations (Thapar, 1999). Apart from these afflictions, there is a decline in prey availability within these shrinking and fragmented habitats. This decline is likely a consequence of habitat degradation and hunting pressure on prey species (Karanth & Stith 1999; Karanth & Sunquist 2000). Poaching for body parts used in traditional medicine and the illegal wildlife trade is also a significant threat (WPSI, 2023). India's tiger conservation story is commendable, but continued efforts to protect existing habitats, create functional corridors, address prey decline, and combat poaching are essential to ensure the long-term survival of this iconic species.

The tiger population in Odisha is alarmingly low, with only an estimated 20 ± 4 individuals; STR serves as a critical refuge (Qureshi *et al.*, 2023). This isolated population faces numerous threats. Poaching remains a constant danger (Jhala *et al.*, 2020), though precise data within the reserve can be challenging to obtain due to its clandestine nature. However, national reports on wildlife crimes in India highlight the severity of the issue (WPSI, 2023). Additionally, habitat degradation and fragmentation caused by human activities like infrastructure development are squeezing the tigers' space and resources (Jhala *et al.*, 2015). This reduces their occupancy and disrupts prey availability and movement patterns, jeopardizing their long-term survival. To secure the future of these magnificent creatures, conservation efforts must be prioritized in STR through population monitoring, habitat evaluation, prey base assessment.

Leopard

The leopard is a globally threatened big cat with one subspecies in Africa and eight Asian subspecies (Hunter, 2015). Leopards are remarkably adaptable big cats, thriving in a wide range of environments, occupying areas with winter lows of -30°C to summer highs exceeding 50°C (Nowell & Jackson, 1996). However, they reach high densities in mesic woodland, grassland savanna, subtropical to tropical dry and humid forests worldwide (Nowell & Jackson, 1996). The leopard's impressive adaptability allows them to survive near human settlements and thrive in modified habitats, highlighting their behavioral plasticity (Atheria *et al.*, 2011; Dhee *et al.*, 2019). Despite having the most extensive geographical distribution among wild felids (Nowell & Jackson, 1996), the leopard faces a grim reality. The leopard has lost a

large part of its historic geographical distribution globally due to anthropogenic factors. It has been extirpated from 63% of its global historic range, with the range loss being more severe in Asia (83-87%) than Africa (48-67% loss) (Jacobson *et al.*, 2016). There are no reliable estimates of the global leopard population. However, based on the severe range constriction, IUCN has changed its conservation status from 'Near Threatened' to 'Vulnerable' in the red list of threatened taxa (Stein *et al.*, 2023).

The eradication of leopards from Asia is evident from the fact that it forms only 22% of the current extant global range despite harboring eight of the nine subspecies. India has a crucial role to play for leopard conservation, accounting for 43% of the remaining distributional range of Asia's leopards (Jacobson *et al.*, 2016). Despite their impressive ability, leopards face several threats. Habitat loss, prey depletion, and poaching all contribute to their decline (Bhatt *et al.*, 2020; Al Hikmani *et al.*, 2023; Shivakumar *et al.*, 2023). The situation is particularly dire in livestock occupied areas, where leopards are often persecuted due to real or perceived threats to livestock (Athreya *et al.*, 2011). Additionally, fear and retaliation killings by humans further compound the issue (Swanepoel *et al.*, 2015). While the threats are explicit, a significant knowledge gap exists regarding leopard population dynamics in the wild (Bailey, 1993; Balme *et al.*, 2009; Chase-Grey *et al.*, 2011; Balme *et al.*, 2013; Swanepoel *et al.*, 2014). A lack of robust data on population trends makes it difficult to assess the true extent of the decline and hinders the development of effective conservation strategies.

India faces a unique challenge in leopard conservation. The Indian leopard subspecies, *Panthera pardus fusca*, has vanished from a staggering 70% of its historical range within the country, exceeding the global average decline (Jacobson *et al.*, 2016). Despite being legally protected under Schedule I of the Wildlife Protection Act (1972), the future of the Indian leopard remains precarious. A recent population estimate suggests approximately 13,874 leopards across 70% of their occupied range within India (Qureshi *et al.*, 2024). However, a significant portion of the leopard population resides outside protected areas, where reliable population estimates are lacking (Athreya *et al.*, 2013; Athreya *et al.*, 2014).

Habitat degradation and fragmentation are major threats to the Indian leopard. Unsustainable human development activities driven by ever-growing demands are a major reason for habitat loss (Qureshi *et al.*, 2024). This habitat loss, in turn, increases the likelihood of negative interactions between humans and leopards, further jeopardizing their survival (Jacobson *et al.*, 2016; Kshetry *et al.*, 2017). The leopard population has plummeted by 75-90% in the last two centuries, primarily due to human activities (Bhatt *et al.*, 2020). Poaching is a major cause, with estimates suggesting a staggering four leopards poached every week in India (Raza *et al.*, 2012). A WPSI report (2023) highlights the severity of the issue, estimating that nearly 1500 leopards were poached in the last decade alone (2013-2022). These alarming trends pose a significant threat to the leopard's survival and disrupt the ecosystem's delicate equilibrium (Qureshi *et al.*, 2024). Consequently, developing and implementing effective conservation strategies are of critical importance. Long-term population monitoring across diverse landscapes is crucial. Studying vital rates (birth and death

rates) is essential to understanding population dynamics (Karanth & Nichols, 2017). In addition to population monitoring, research on habitat use, diet, natural history, and behavior is necessary to develop comprehensive management plans. Only through a holistic approach that addresses poaching, habitat loss, and a deeper understanding of leopard ecology can India hope to secure the future of this magnificent species.

Competition and coexistence of tigers and leopards

The survival of top predators in natural ecosystems hinges on a delicate balance. Competition between species occupying similar roles (called "intra-guild competition") can significantly affect population dynamics (Palomeres & Caro, 1999; Linnell & Strand, 2000; Caro & Stoner, 2003). Species occupying similar niches in an environment rarely coexist; this often leads to "competitive exclusion," where one species outcompetes the other (Gause, 1934). Interestingly, physical differences may evolve when these species coexist to minimize competition. This phenomenon, called "ecological character displacement," involves changes in size or shape to reduce overlap in resource use (Brown & Wilson, 1956). Hutchinson (1959) further explored this concept by questioning why many different animal species exist. He argued that ecologically similar species with identical body structures could not coexist in the long run. This theory led to the developing "Hutchinson ratios," which measure the minimum morphological (physical) differences required between potential competitors to avoid resource competition.

Carnivores, with their wide-ranging habitats and remarkable variation in body size, have been a focal point for research on character displacement (Ralls & Harvey, 1985;

Dayan *et al.*, 1990; VanValkenburgh & Wayne, 1994; Simberloff *et al.*, 2000; Davies *et al.*, 2007). The interspecific competition between species is a significant factor limiting the number of carnivores that can coexist in a particular habitat, as they often share similar ecological roles (Di Bitetti *et al.*, 2010). Higher densities of large predators increase the chances of encountering subordinate carnivores, forcing the latter to avoid certain areas (Ramesh *et al.*, 2012). In sympatric large carnivore guild, dominant species can significantly reduce the numbers of subordinate competitors, even driving them to extinction (Palomares & Caro, 1999; Vucetich & Creel, 1999; Caro & Stoner, 2003). Changes in demographic parameters such as reduction in densities, growth, fecundity, altered age structure at the population level are the outputs observed due to intra-guild competition (MacNally, 1983; Petren & Case, 1998). The interspecific competition in carnivores usually increases when the diet schemes and adaptations of morphological features are similar (Morin, 1999). Thus, competition between two or more carnivore species is bound to intensify with increased similarity in diet and physical adaptations. Larger carnivores, which require substantial energy to hunt larger prey, face an elevated risk of kleiptoparasitism from competitors leading to intensified competition (Wang *et al.*, 2004).

To mitigate this competition, carnivores have evolved various strategies. Species with similar body shapes may become active at different times of the day or utilize different areas within the same habitat, minimizing overlap in resource use (Pianka, 1974; Schoener, 1974; Durant, 1998; Linnell & Strand, 2000; Harrington *et al.*, 2009). For medium and small-sized carnivores, forming groups offers a distinct advantage. Group living provides these carnivores with stronger defense and enhanced

competitive ability (Eaton, 1979; Lamprecht, 1981; Gittleman, 1989). Large carnivores may occupy different dietary niches based on their body size, hunting behavior and social organization, time of activity, habitat use, principal prey (Gittleman, 1985; Karanth & Sunquist, 1995; Ramakrishnan *et al.*, 1999; Hayward & Kerley, 2008). Moreover, the habitat structure or habitat heterogeneity also affects the intensity of interactions among the sympatric carnivores in the guild (Warfe & Barmuta, 2004; Finke & Denno, 2006). In Africa, lions are the most dominant predators (Owen-Smith & Mills, 2008). They claim the most productive territories, rich in resources (Vanak *et al.*, 2013). Small carnivores avoid these prime areas, fearing dominant predators (Chesson, 1986). However, some studies suggest that subordinate carnivores might risk using the same areas as dominant predators, potentially trading-off safety for better hunting opportunities rather than face starvation in suboptimal habitats (Vanak *et al.*, 2013).

In many parts of Asia, the tiger and leopard are sympatric (Seidensticker, 1976). With, the tigers being four time the size of leopards (Seidensticker, 1976); leopard populations tend to be lower in areas where tiger is abundant (Schaller, 1967; Johnsingh *et al.*, 2004). This dominance is likely due to the tiger's larger size (Karanth & Sunquist, 1995). While confrontations are rare, the threat of being attacked can still significantly affect leopards (Harihar *et al.*, 2011). This risk can lead to avoidance of areas and times when dominant predator is active (Lima & Dill, 1990). The indirect effects of this threat, such as restricted habitat use, can be just as detrimental to leopard survival as direct encounters (Preisser *et al.*, 2005; Creel & Christianson, 2007; Ritchie & Johnson, 2009). Studies have shown leopards avoiding areas with

tigers and shifting to the peripheries of protected areas (Seidensticker, 1976; Mondal *et al.*, 2012). For example, reintroducing tigers in Sariska National Park led to a decline in the leopard population and a shift in their space use was observed from tiger-dominated areas (Mondal *et al.*, 2012).

Leopards and tigers coexist due to niche partitioning (Karanth & Sunquist, 1995; Andheria *et al.*, 2007). Despite similar body size differences, leopards and tigers partition resources by targeting different prey size classes (Karanth & Sunquist, 1995). However, studies show an 89-98% overlap in their prey base, consisting of ungulates like sambar and chital (Karanth & Sunquist, 1995; Edgaonkar, 2008; Ramesh *et al.*, 2009; Harihar *et al.*, 2011; Majumder *et al.*, 2013; Selvan *et al.*, 2013). Leopards, being smaller, target smaller prey and excel at hunting primates due to their arboreal nature and agility (Karanth & Sunquist, 1995; Sankar & Johnsingh, 2002; Andheria *et al.*, 2007; Wang & Macdonald, 2009). Predators may also exhibit some preference within a shared prey species. Males of most ungulates are usually solitary, are more vulnerable and susceptible to predation compared to females in groups (Schaller, 1967; Johnsingh, 1983; Karanth & Sunquist, 1992). Interestingly, studies from Pench Tiger Reserve (Majumder *et al.*, 2013) and Nagarhole National Park (Karanth & Sunquist, 1995) suggest tigers may target healthier prey than leopards due to their larger size. Nevertheless, this was not observed in the Mudumalai Tiger Reserve (Ramesh, 2010).

Like other large carnivore communities, tigers and leopards may also exhibit temporal segregation to minimize competition (Scognamillo *et al.*, 2003; Harmsen *et al.*, 2009).

For instance, in Sariska Tiger Reserve, leopard activity significantly increased in the evenings after tigers were extirpated from the area. However, upon tiger reintroduction, leopards shifted their activity to late evenings, avoiding the peak activity period of tigers (Mondal *et al.*, 2012). This strategic adjustment in activity patterns allows leopards to utilize prey resources at different times of the day, promoting coexistence within the shared habitat. It enables one species to make way for the competitor by shifting its activity times to reduce encounters (Mondal *et al.*, 2012). However, no such differences between the tiger and leopard activity pattern were observed in Mudumalai Tiger Reserve (Ramesh *et al.*, 2012).

Understanding the ecological relationships and coexistence mechanisms within large carnivore guilds is crucial for conservation efforts, especially considering the vulnerability of top predators to extinction (Purvis *et al.*, 2000). Top predators play a vital role in maintaining healthy ecosystems by regulating prey populations (Estes *et al.*, 2011). Their presence can also influence the behavior of other species, leading to a cascading effect throughout the ecosystem. For instance, the fear of predation by wolves can cause deer to alter their grazing patterns, promoting plant diversity (Beschta & Ripple, 2016). However, human activities such as habitat loss, poaching, and prey base depletion push many top predators toward extinction. This decline in top predator populations can have severe consequences for the overall health of ecosystems. Conservationists can develop more informed strategies for protecting these keystone species and the ecosystems they depend on by studying the factors that enable coexistence among large carnivores.

India, a nation with a large human population and its demand for development, has significantly reduced the average size of its protected areas (Wildlife Institute of India, 2023). These protected areas are often islands within a sea of human-dominated landscapes (Jhala *et al.*, 2008). Despite this, suitable habitat remains in India to accommodate more tigers (Jhala *et al.*, 2019). However, STR in Odisha has shown a drastic decrease in tiger occupancy between 2006 and 2014 (Jhala *et al.*, 2008; Jhala *et al.*, 2011; Jhala *et al.*, 2015). Odisha's tiger population, now primarily confined to STR, is genetically unique and warrants priority conservation investment (Kolipakam *et al.*, 2019). The tiger and the sympatric leopard population also show a declining trend in Odisha (Qureshi *et al.*, 2023; Qureshi *et al.*, 2024).

This study investigates the crucial aspect of coexistence for large predators like tigers and leopards sharing the same landscape and delves into the population dynamics of these animals by identifying the mechanisms of resource partitioning. By acting as a window into the inner workings of the ecosystem, the study reveals how tiger and leopard populations function alongside each other. Identifying the factors that influence their ability to share the resources successfully is vital for developing more effective conservation strategies. This knowledge ultimately contributes to ensuring the long-term survival of both tigers and leopards in this landscape. A precise assessment of several demographic parameters is necessary to make informed management decisions for their conservation within this unique habitat. These parameters include population density, sex structure, recruitment, and survival rates. Furthermore, understanding prey selection patterns for both predator species is

crucial. This comprehensive understanding will be fundamental for developing effective conservation strategies for tiger and leopard population.

With this background, the study comes with the following objectives.

Objectives

- (1) To assess the abundance and spatial distribution of prey in STR.
- (2) To assess the various demographic parameters of large felids (tiger and leopard) in STR.
- (3) To determine the mechanisms of resource partitioning of the tiger and the leopard in STR.

Study Area

Similipal Tiger Reserve is located in the Mayurbhanj district of Odisha, between 86°06' and 86°36' East longitude and 21°31' and 22°02' North latitude. Positioned in the northern part of Odisha within the Deccan Peninsula biogeographic zone, it falls under the Chhotanagpur Biotic Province and the Mahanadian Biogeographical Region (Rodgers & Panwar, 1988). Established in 1973, STR is one of the first nine tiger reserves in India and is currently the fifth largest in the country (NTCA, 2024), covering an area of 2750 km² with a core area of 1194.75 km² and a buffer area of 1555.25 km² (Upadhyay *et al.*, 2012; Nayak, 2014). The core area comprises of only one village, Bakua, while the buffer zone includes 65 villages (Nayak, 2014; Dash & Behera, 2018). STR has been a part of the Global Network of Biosphere Reserves since 2009 due to its distinct ecosystem, cultural, and ecological diversity. In the same year, Left-Wing Extremists (LWE) carried out a series of attacks from March 28 to

April 15, severely damaging the infrastructure and forest management. Two years later, normalcy began to return in STR (Nayak, 2014).

The landscape of STR is predominantly hilly and undulating, interspersed with grasslands and forests with the highest elevation at 1168 meters above sea level (Nayak, 2014). The climate is subtropical, defined by a hot summer, evenly spaced rainfall, and a typical winter (Nayak, 2014). The winter season runs from October to February, and the summer season from March to June. Between July and September, there is a noticeable monsoon. The post-monsoon season lasts until October (Palei *et al.*, 2015). With an average annual rainfall between 1200-2000 mm, Simlipal has a moist landscape comprising a matrix of many perennial water streams, even half-active during the driest months of the year (Das *et al.*, 2012; Nayak, 2014). The primary rivers of STR are West Deo, East Deo, Budhabalanga, Palpala, Khadkei, and Khairi (Das *et al.*, 2012; Nayak, 2014; Mishra *et al.*, 2019). The region is climatically hot, with northern Simlipal comparatively drier than southern Simlipal. The landscape has a temperature range of 4 to 35° and a relative humidity of 70%. (Nayak, 2014).

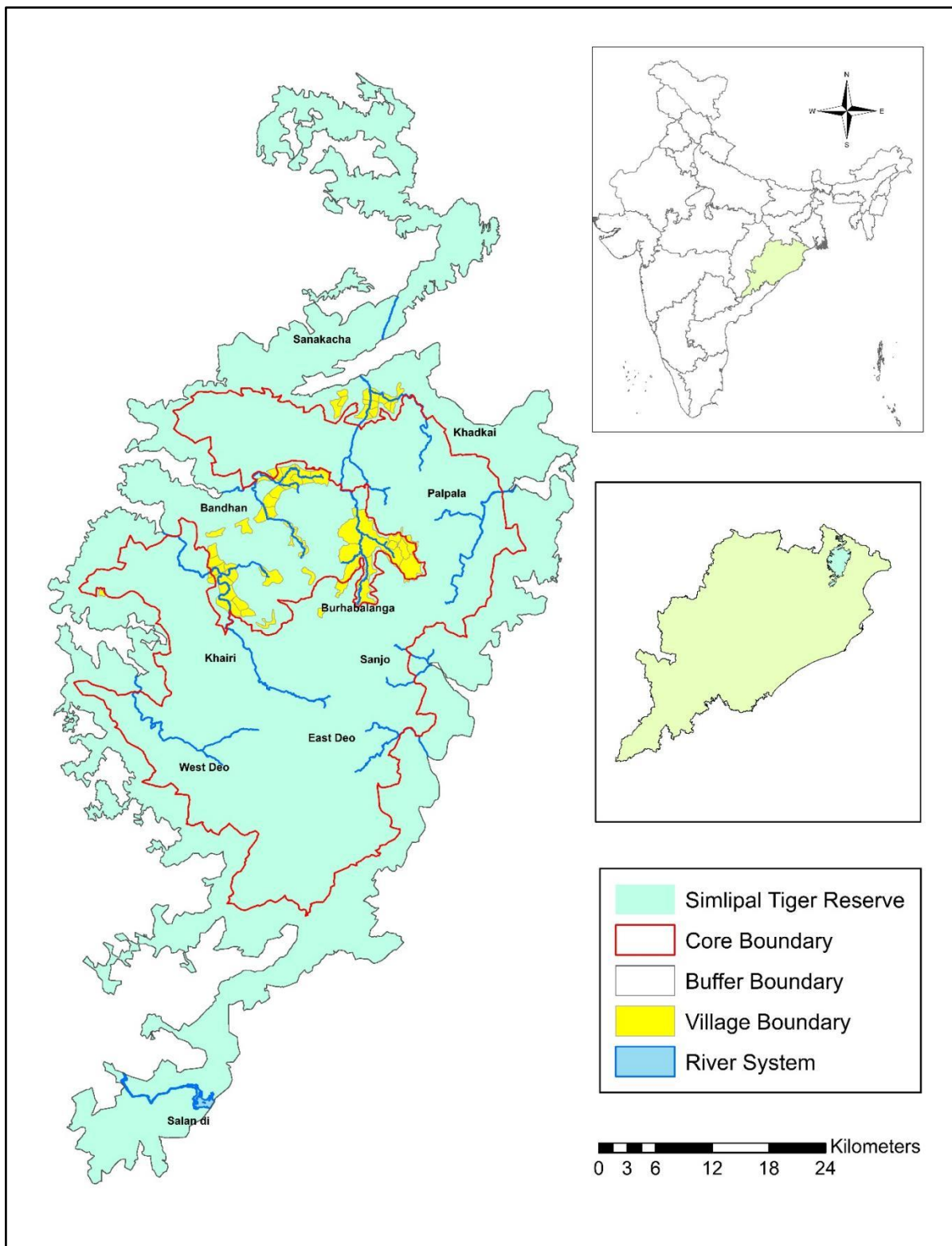


Figure 1.1. Study Area

The vast expanse of forest is uniquely composed of different forest types, such as northern tropical mixed deciduous forest, northern tropical semi-evergreen forest, mixed deciduous hill forest, high-level sal forest, dry deciduous sal forest, plain sal forest, grassland, and savannahs. The primary forest type here is Northern Tropical Moist Deciduous Forest, which constitutes the largest area of about 1540 km², and Northern Tropical Semi-evergreen Forest with an area of 80 km², along with Dry Deciduous Hill Forest and High-Level Sal Forest, which extends over an area of 250 km² each. Grassland and Savannah constitute a small area of < 10 km² (Champion & Seth, 1968; Das et. al., 2008). STR is an important source of the population of tigers in Odisha (Walston *et al.*, 2010) connected with the neighboring protected areas through corridors. The important identified corridors in the landscape are Simlipal-Kuldiha corridor which connects Similipal with Hadagarh Wildlife Sanctuary of Keonjhar Wildlife Division and further to Kuldiha Wildlife Sanctuary of Balasore Wildlife Division. The Simlipal-Badampahar corridor connects STR with Badampahar Reserve Forest. Similipal Tiger Reserve is connected to Satkosia Tiger Reserve through Simlipal- Satkosia corridor (Nayak, 2014; Qureshi *et al.*, 2014). These corridors provide immense opportunities to prevent the negative impacts of habitat fragmentation and degradation, such as genetic isolation of population, animal dispersal, ecological restoration, and minimizing man-animal conflict in the area.



Figure 1.2. “Joranda waterfall” landscape in STR.

Simlipal is an indigenous knowledge repository crucial for traditional ecological understanding and biodiversity conservation. It is home to numerous primitive tribes of Odisha, including the Hill Khadias, Birhors, and Ujias, whose livelihood depends directly on the forest (Dash & Bahera, 2018). Once the hunting ground of the Maharaja of Mayurbhanj, Simlipal has a long history marred by vilified cases of mass hunting rituals known to the locals as ‘Akhand Shikar’ (Nayak, 2014). However, nowadays, people's daily livelihoods rely directly on the forest (Dash & Bahera, 2018), encouraging community-based landscape conservation.

Simlipal is a high-profile tiger reserve with the only abode for unique melanistic tigers worldwide (Jhala *et al.*, 2019; Sagar *et al.*, 2021). It also holds 1253 species of flowering plants, 361 species of birds, 62 species of reptiles, 55 species of mammals, and 21 species of amphibians (Upadhyay *et al.*, 2012; Nayak, 2014). STR is also

famous for its largest tiger population in Odisha and its sizable population of Asian elephants (*Elephas maximus*). The other large carnivores found in STR are the leopard (*Panthera pardus*), dhole (*Cuon alpinus*), sloth bear (*Melursus ursinus*), and wolf (*Canis lupus*). The potential prey species of these large carnivores in the study area are chital (*Axis axis*), sambar (*Rusa unicolor*), gaur (*Bos gaurus*), chowsingha (*Tetracerus quadricornis*), northern red muntjac (*Muntiacus vaginalis*), wild pig (*Sus scrofa*), mouse deer (*Moschiola indica*), Hanuman langur (*Semnopithecus entellus*), Indian crested porcupine (*Hystrix indica*), Indian peafowl (*Pavo cristatus*), rhesus macaque (*Macaca mulatta*), and Indian hare (*Lepus nigricollis*) (Palei *et al.*, 2015). The other threatened animals found in STR are the Indian pangolin (*Manis crassi caudata*) (endangered), small-clawed otter (*Aonyx cinrea*) (vulnerable), and mugger (*Crocodylus palustris*) (vulnerable) (Nayak, 2014). Similipal is also home to 98 species of orchids, of which three are endemic to the region, including *Bulbophyllum panigrahanum*, and *Eria meghasaniensis*. STR is ecologically distinct as it possesses floral and faunal components similar to those of the Himalayas, Western Ghats, and Northeast India (Nayak, 2014).

Due to its diverse vegetation and the ability to support a high density and biomass of prey, along with the presence of villages within the park, it offers excellent opportunities for research on the population dynamics of tigers, co-predators, and their prey. The study was carried out over three years (2019–2021) across eight ranges in the core area of STR: Chahala, Nawana North, Nawana South, and Pithabata South



A. Leopard



B. Tiger



C. Elephant Herd



D. Chital Herd

Figure 1.3. Faunal diversity of STR.

Wildlife in the northern core, and UBK, Jenabil, Bhanjabasa, and National Park in the southern core. In 2022, apart from the ranges mentioned above, the core regions of the Thakurmunda WL, Kendumundi WL, and Gurguria WL ranges were added to the study area. The ungulate abundance was estimated in the entire core from 2019 to 2021 to assess their population trend. In 2021, the transect lines were also walked in the buffer zone to arrive at the ungulate densities for the entire tiger reserve. However, the camera trapping was conducted in only the core zone of Similipal Tiger Reserve during the entire sampling duration.



Chapter - 2

Abundance and Spatial Distribution of Prey in Similipal Tiger Reserve

Introduction

The scientific knowledge on various tropical ungulates is lacking despite their crucial role in regulating ecosystem functions through herbivory, dispersal of seeds, nutrient cycling, and acting as a food resource for large carnivores (McNaughton *et al.*, 1997; Murray *et al.*, 2013; Gray, 2018). Tropical forests can harbour high ungulate biomass and abundant large-bodied prey, forming an unchallenged component for sustaining a viable population of large carnivores (Karanth & Stith, 1999). However, the depletion of prey is one of the principal reasons that led to the decline of large carnivores, i.e., the tiger and the leopard, in India (Karanth *et al.*, 2004; Jhala *et al.*, 2019; Castello, 2020). Almost 50% of mammalian prey predated upon by tigers are under extinction threat, and ~80% are undergoing a decline in populations (Wolf & Ripple, 2016). It has been observed that large carnivore densities are positively correlated with prey density (Karanth *et al.*, 2004; Searle *et al.*, 2021). Thus, it becomes extremely critical to assess prey population metrics to develop targeted intervention actions aiming at large carnivore conservation (Karanth & Nichols, 2017).

The East-Central landscape comprising the Indian states of Chhattisgarh, Jharkhand, and Odisha has also seen a continuous decline in large felid abundance (Jhala *et al.*, 2021; Qureshi *et al.*, 2024). The state of Odisha, where Similipal Tiger Reserve is situated, has seen a continuous decline in tiger and leopard populations (Jhala *et al.*,

2021; Qureshi *et al.*, 2023; Qureshi *et al.*, 2024). The illegal consumption of bush meat by the local community and the consequential decline of prey species in this region has been identified as the major reason for forested regions being devoid of tigers (Nayak, 2014; Jhala *et al.*, 2021). The snares laid for hunting ungulates have been known to kill large carnivores (Jhala *et al.*, 2021). The landscape could support multiple viable populations of tigers given that the prey populations are restored in the landscape and protection assured (Jhala *et al.*, 2021).

Similipal Tiger Reserve is the last known breeding population from the entire East-central landscape (Rathore *et al.*, 2021) and currently is the only place globally to host pseudo-melanistic tigers (Jhala *et al.*, 2015; Kolipakam *et al.*, 2019; Sagar *et al.*, 2021). The leopard population has dwindled in Odisha in the past four years (Qureshi *et al.*, 2024). Similipal, with its enormous size, is currently the best potential habitat for tigers and leopards in Odisha. Thus, continuous monitoring of prey base to assess their densities and population trends is vital. Moreover, understanding factors governing the spatial distribution of large carnivore prey is also crucial to suggest scientific managerial recommendations and actions.

Methods

Density estimation and population trend of large carnivore prey in Similipal Tiger Reserve

The density of large carnivore prey was assessed using a well-established DISTANCE sampling technique known as the line-transect method (Burnham *et al.*, 1980). Line transects (each 2 km in length) were systematically laid in the entirety of Similipal Tiger Reserve. The line transects were distributed across the study area with, one in

each forest beat (smallest administrative unit) incorporating the tiger reserve's core and buffer zone. This strategy ensured comprehensive spatial coverage in each habitat type throughout the study area. Transect lines were laid to minimize habitat alteration and avoid creating artificial clearing that could attract ungulates. The width of these transects was carefully managed to ensure only sufficient walking space for two observers. I surveyed the entire reserve with a team of trained and tested forest department staff who were well-versed in field craft and species identification. Each line transect was walked on four separate days during the early morning period (between 5:30 AM- 8:00 AM) as the ungulate activity levels are presumed to be lower after this period due to the rising temperatures.

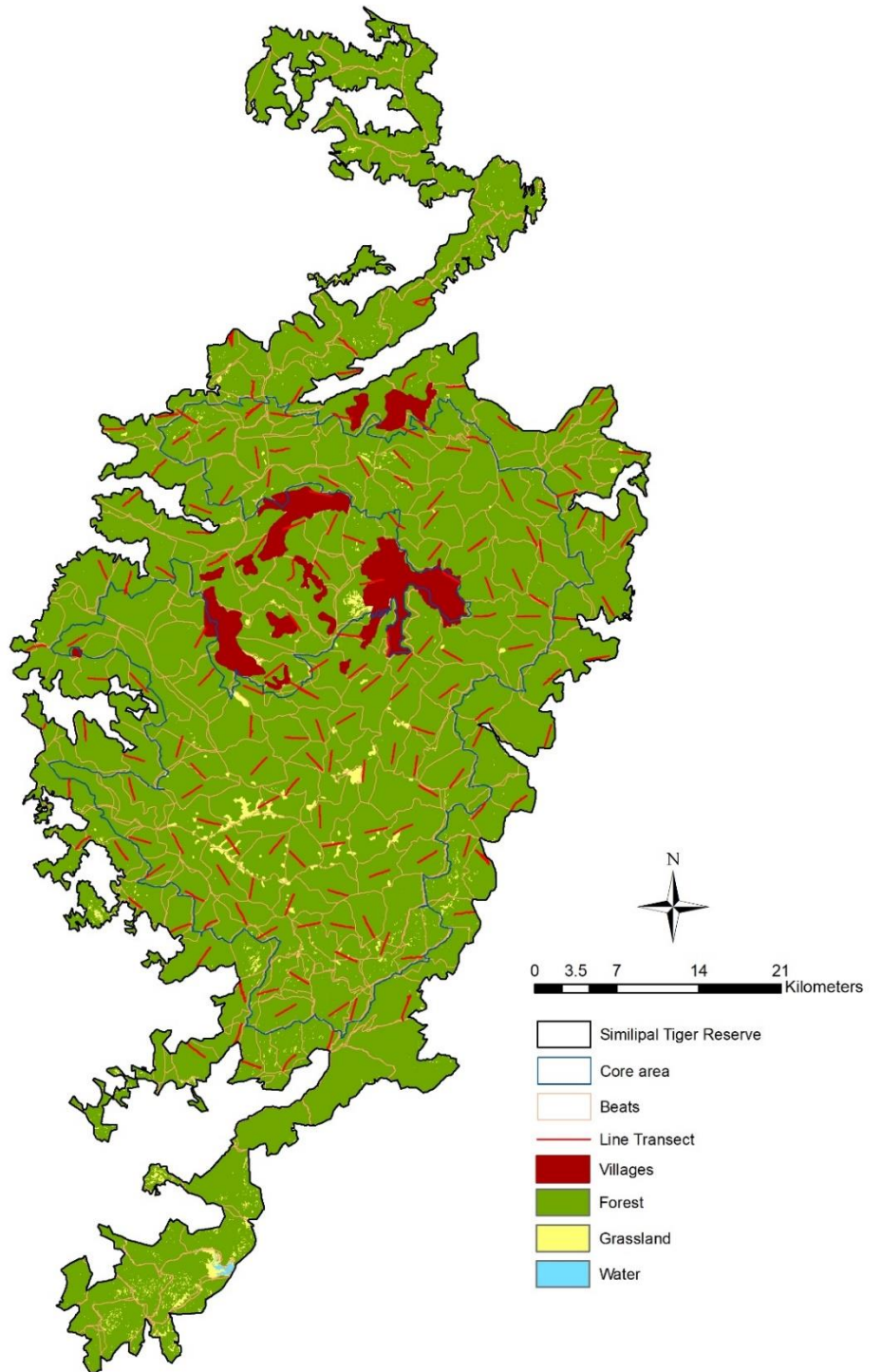


Figure 2.1. A systematic layout of transect lines in Similipal Tiger Reserve.

For each ungulate sighting, following parameters were recorded:

- Species ID
- Date and time of sighting
- Sighting distance
- Group size
- Animal bearing and walk bearing
- Major Habitat type
- Terrain Type- Flat, undulating and very undulating
- The Global positioning System (GPS) reading of the beginning and end point of the transect.

I measured the radial distance using the laser rangefinder (Nikon Forestry Pro) and recorded the animal's bearing by using SUUNTO see-through compass.

I used the software program Distance 7.5 (Thomas *et al.*, 2010) to analyse the data for estimating the population density of the major prey species in STR. Analysis was conducted at the cluster size level, as data on individual animals is likely to underestimate the true population variance (Southwell & Weaver, 1993). To understand how often animals were spotted at different distances from transect lines, we grouped the sighting distances into small ranges. We created histograms of these groupings, as recommended by Buckland *et al.*, (2001). After examining the resting histograms, I truncated the data for each species to a suitable maximum distance. The signs of piling, spikes near the line, avoidance movements, and steep fall away from the line were also examined. The sighting distance for each species was then recognized into suitable categories to ensure the detection function accurately

reflected the probability of spotting animals. Different models, including half-normal, hazard rate, and uniform, were applied to each species along with functions like Hermite polynomials, simple polynomials, and cosine series. I chose the model with the lowest Akaike Information Criterion (AIC) value (Burnham & Anderson, 2002) as the best fit for each species.

Factors governing spatial distribution of large carnivore prey in Similipal Tiger Reserve

I used the entire distance data for density surface modeling (DSM) to assess the distribution of different ungulate species in STR. These spatially explicit models, i.e., Density Surface models (DSM), are useful for studying how animal populations respond to various ecological/ environmental factors that differ across the study area. This model, which considers animal locations (spatially explicit model), can account for the differences observed between transects. This leads to a more precise estimate of animal abundance (Miller *et al.*, 2013). I used density surface modeling in a two-step process. First, I modeled how well we detect animals at different distances (i.e., detection function). Then, I used this information to build a model that considers animal locations across the study area (i.e. spatial model).

1st stage- Modelling the detection function:

Distance sampling acknowledges the inherent limitations in animal detection during surveys (Buckland *et al.*, 2001; Buckland *et al.*, 2004). To account for this, a mathematical function, $g(x)$, is employed to model the decline in the probability of detecting an animal as the distance from the observer increases (Buckland *et al.*, 2001; Miller *et al.*, 2013). The detection function, $g(x)$, characterized the probability

of observing an animal at a given distance x from the transect line. The initial stage of the investigation employed the Distance package (Miller *et al.*, 2019) in the R programming environment (R Development Core Team 2023) to quantify both the density and abundance of the ungulate population. An evaluation was conducted of three primary detection function models: uniform, half-normal, and hazard-rate. Additionally, each model was assessed in conjunction with three adjustment terms: Hermite polynomial, cosine, and simple polynomial. The selection of the most suitable detection function was guided by the Akaike Information Criterion (AIC; Akaike, 1974). This choice was further supported by examining visual representations of the distance data (histograms) and applying statistical tests to assess model fit (Burnham *et al.*, 1980). The outcomes of the density surface modeling rely upon the most parsimonious detection function identified during the initial phase of the study.

2nd stage- Density surface modelling

This stage of the analysis was also conducted within the R statistical environment (R Development Core Team, 2023) utilizing the dsm package (Miller *et al.*, 2022). Line transects were subdivided into contiguous segments of 250 meters. Subsequently, buffer zones were generated from the central point of each of these segments using ArcGIS 10.0. Density estimations were conducted at a spatial resolution of 250 meters, encompassing 5,270 segments. The analysis employed a well-established count method for estimating animal abundance within discrete spatial units (Hedley & Buckland, 2004). This approach utilized the number of animals observed in each segment as the dependent variable within the density surface model. Seven

ecological/environmental variables at the observation level were extracted from remotely sensed data using ArcGIS software. These variables included:

- Normalized Difference Vegetation Index (NDVI_diff)- It is the difference between NDVI November and November April and is an index of year-round availability of green cover- Derived from Sentinel- 2 dataset (10 m resolution)
- Distance to villages (Dist_vil)- Eucliden distance
- Aridity index- Derived from primary data
- Elevation- Digital elevation data (30 m resolution) from SRTM version 4.1
- Terrain ruggedness- Derived from Digital Elevation Model
- Distance to meadows/ grasslands (Dst_meadow)- Euclidean distance
- Distance to water- Euclidean distance
- NDVI (November)- Derived from Sentinel- 2 dataset (10 m resolution)
- NDVI (April)- Derived from Sentinel- 2 dataset (10 m resolution)

The relationship between the number of animals observed within each segment (dependent variable) and the environmental predictor variables was modeled using Generalized Additive Models (GAMs) (Hastie & Tibshirani, 1990). This analysis employed a tweedie distribution and a logarithmic link function. Selection of the appropriate density surface model was guided by a combination of factors: the lowest Akaike Information Criterion (AIC) value, the proportion of variance explained by each model, alignment with ecological principles (plausibility), and the statistical significance (p-value) of each environmental predictor variable included in the model.

I generated a high-resolution prediction grid of 0.0625 km² (250 meters x 250 meters) using ArcGIS. The total population abundance of ungulates within the study area is the sum of the estimated abundance values across each grid cell. This calculation relies upon the selected spatial model for generating these abundance inferences. Leveraging the abundance predictions generated by the density surface model, an abundance map for each ungulate species across the entire Similipal Tiger Reserve was created using the R statistical environment (R Development Core Team, 2023). The variance associated with abundance estimates derived from the DSM analysis was determined by employing the variance propagation method outlined by Williams *et al.*, (2011). This method facilitates the rapid estimation of variance.

Results

Density estimation and population trend of large carnivore prey in Similipal Tiger Reserve

The prey abundance estimation in Similipal Tiger Reserve for years 2019, 2020, and 2021 was conducted through distance sampling on line transects. In the core area of Similipal, the exercise was conducted with a walk effort of 319.75 km (n=39 line transects), 608 km (n= 71 line transects), and 754 km (n = 95 line transects) in 2019, 2020 and 2021 respectively. In 2021, the line transects were also walked in the buffer region to assess the density. Thus, in total, 158 line transects were walked in the entire Similipal Tiger Reserve with an effort of 1243 km to assess the density of major prey species in an entire protected area. Field data from the line transect were recorded for seven prey species: chital, sambar, Hanuman

langur, wild pig, and Northern red muntjac. Although gaur and mouse deer were also sighted on the line transects but their observations were too low to get any ecological inferences. Thus, they were not considered during analysis (Buckland *et al.*, 2001). All the beats in which the transect lines were in the vicinity of artificial salt-licks in Similipal were not considered for the data analysis as the observations on the transect would be biased.

The results of the DISTANCE 6.2 (Thomas *et al.*, 2010) for the estimate of prey density in the core of Similipal Tiger Reserve for 2019, 2020 and 2021 are shown in (Table 2.1, Table 2.2 & Table 2.3) below. A separate prey density analysis was also conducted for the Northern core and Southern core in 2021 (Table 2.4 & Table 2.5). The prey density estimates for the buffer zone in 2021 are mentioned in (Table 2.6). In 2021, an estimate of prey densities for the entire STR was also generated (Table 2.7). The result tables show the number of detections, estimated density of clusters, estimated cluster size (mean cluster size where there was no size bias in detection), and mean density of individuals, percent coefficient of variation. The model with the lowest AIC value was considered the best fit model.

Table 2.1. Model Statistics and parameter estimates of line transect (n = 39, Total effort 287.52 km) based distance sampling for prey species in the core of Similipal Tiger Reserve, 2019).

Species	Best Model	Chi square χ^2	No. of observations (n)	Effective strip Width (ESW) [SE]	Encounter rate (n/l) [%CV]	Detection probability [SE]	Cluster size density [SE]	Mean Cluster Size [SE]	Density [SE]
Chital	Hazard Rate-Simple Polynomial	0.899	37	34.47 [6.79]	0.12 [31.55]	0.27 [0.05]	1.86 [0.69]	5.82 [0.66]	10.87 [4.23]
Sambar	Half- normal Cosine	0.993	69	31.74 [3.27]	0.23 [20.51]	0.52 [0.05]	3.77 [0.86]	3.31 [0.29]	12.53 [3.07]
Northern Red Muntjac	Hazard Rate-Simple Polynomial	0.957	108	27.07 [1.89]	0.37 [14.38]	0.45 [0.03]	6.93 [1.10]	1.13 [0.02]	7.90 [1.27]
Hanuman Langur	Hazard Rate-Simple Polynomial	0.950	82	39.43 [3.79]	0.28 [16.94]	0.56 [0.05]	3.61 [0.70]	5.79 [0.50]	20.93 [4.47]
Wild Pig	Half- normal Cosine	0.901	13	32.21 [8.74]	0.04 [32.07]	0.71 [0.19]	0.70 [0.29]	5.06 [1.80]	3.55 [1.95]

The density of chital, sambar, wild pig, Northern red muntjac, and Hanuman langur did not show any significant change in the three sampling years in the core and remained similar between 2019, 2020, and 2021 (Figure 2.2). The density estimate for chital was $10.87 \pm 4.23/ \text{km}^2$ in 2019, $10.93 \pm 2.64/ \text{km}^2$ in 2020 and $9.92 \pm 2.31/ \text{km}^2$ in 2021. In 2019 and 2020, the density of sambar was estimated at, i.e., $12.53 \pm 3.07/ \text{km}^2$ and $10.33 \pm 1.89/ \text{km}^2$ respectively. The sambar density stood at $8.61 \pm 1.56/ \text{km}^2$ in 2021. Northern red muntjac had a very high density in Similipal Tiger Reserve. However, the density of northern red muntjac remained similar throughout the study period, i.e., $7.90 \pm 1.27/ \text{km}^2$ in 2019, $7.38 \pm 0.98/ \text{km}^2$ in 2020, and $6.44 \pm 0.75/ \text{km}^2$ in 2021. Hanuman langur had a density of $20.93 \pm 4.47/ \text{km}^2$, $22.47 \pm 3.71/ \text{km}^2$, and $19.66 \pm 2.89/ \text{km}^2$ in the year 2019, 2020 and 2021 respectively. The

number of observations of wild pigs was very few ($n = 13$) to arrive at a reliable estimate of their density in 2019. However, an attempt was made to assess their density with limited observations, but the results cannot be relied upon entirely (Table 2.1). The number of observations was sufficient to arrive at the density estimate of wild pigs in 2020 and 2021. The density of wild pig in the years 2020 and 2021 was estimated at $4.86 \pm 1.47/ \text{km}^2$ and $6.07 \pm 1.41/ \text{km}^2$ respectively.

Table 2.2. Model Statistics and parameter estimates of line transect ($n = 71$, Total effort 568 km) based distance sampling for prey species in the core of Similipal Tiger Reserve, 2020.

Species	Best Model	Chi square px2	No. of observations (n)	Effective strip Width (ESW) [S.E]	Encounter rate (n/l) [%CV]	Detection probability [SE]	Cluster size density [SE]	Mean Cluster Size [SE]	Density [SE]
Chital	Hazard Rate-Simple Polynomial	0.919	72	32.05 [3.23]	0.12 [20.51]	0.45 [0.04]	1.97 [0.45]	5.52 [0.43]	10.93 [2.64]
Sambar	Hazard Rate-Simple Polynomial	0.947	105	25.02 [2.57]	0.18 [14.15]	0.44 [0.04]	3.69 [0.64]	2.79 [0.15]	10.33 [1.89]
Northern Red Muntjac	Hazard Rate-Simple Polynomial	0.964	179	24.52 [1.33]	0.31 [12.12]	0.32 [0.01]	6.42 [0.85]	1.14 [0.02]	7.38 [0.98]
Hanuman Langur	Hazard Rate-cosine	0.730	118	26.79 [2.27]	0.20 [11.64]	0.42 [0.03]	3.87 [0.55]	5.79 [0.46]	22.47 [3.71]
Wild Pig	Half-normal Cosine	0.951	36	21.38 [2.82]	0.05 [23.55]	0.44 [0.05]	1.38 [0.37]	3.51 [0.48]	4.86 [1.47]

Table 2.3. Model Statistics and parameter estimates of line transect ($n = 95$, Total effort 754 km) based distance sampling for prey species in the core of Similipal Tiger Reserve, 2021. [SE] =Standard Error.

Species	Best Model	Chi square χ^2	No. of observations (n)	Effective strip Width (ESW) [SE]	Encounter rate (n/l) [%CV]	Detection probability [SE]	Cluster size density [SE]	Mean Cluster Size [SE]	Density [SE]
Chital	Hazard cosine	0.935	72	27.37 [3.26]	0.09 [18.80]	0.31 [0.03]	1.74 [0.38]	5.68 [0.40]	9.92 [2.31]
Sambar	Hazard Simple Polynomial	0.916	119	23.76 [2.20]	0.15 [14.11]	0.36 [0.03]	3.32 [0.56]	2.59 [0.17]	8.61 [1.56]
Northern Red Muntjac	Hazard cosine	0.946	188	20.65 [1.39]	0.24 [9.38]	0.21 [0.01]	6.03 [0.69]	1.06 [0.014]	6.44 [0.75]
Hanuman Langur	Half-normal Hermite Polynomial	0.915	132	24.97 [1.34]	0.17 [11.87]	0.33 [0.01]	3.50 [0.45]	5.61 [0.38]	19.66 [2.89]
Wild Pig	Half-normal cosine	0.891	48	24.36 [2.62]	0.06 [14.76]	0.46 [0.05]	1.30 [0.23]	4.65 [0.66]	6.07 [1.41]

Table 2.4. Model Statistics and parameter estimates of line transect ($n = 39$, Total effort 308 km) based distance sampling for prey species in the northern core of Similipal Tiger Reserve, 2021. [SE] =Standard Error.

Species	Best Model	Chi square χ^2	No. of observations (n)	Effective strip Width (ESW) [SE]	Encounter rate (n/l) [%CV]	Detection probability [SE]	Cluster size density [SE]	Mean Cluster Size [SE]	Density [SE]
Chital	Half-normal cosine	0.871	14	20.84 [4.21]	0.04 [42.28]	0.58 [0.11]	1.09 [0.51]	6.73 [0.92]	7.34 [3.58]
Sambar	Half-normal cosine	0.896	19	26.90 [4.70]	0.06 [25.02]	0.63 [0.11]	1.14 [0.34]	1.73 [0.19]	1.98 [0.64]
Northern Red Muntjac	Half-normal cosine	0.988	52	24.02 [2.66]	0.16 [17.33]	0.55 [0.06]	3.51 [0.72]	0.99 [0.02]	3.50 [0.72]
Hanuman Langur	Half-normal Hermite Polynomial	0.817	52	26.42 [3.00]	0.16 [17.62]	0.61 [0.06]	3.19 [0.66]	5.65 [0.61]	18.06 [4.26]
Wild pig	Half-normal cosine	0.923	16	24.01 [3.29]	0.05 [23.26]	0.46 [0.06]	1.08 [0.29]	5.74 [1.71]	6.21 [2.49]

Table 2.5. Model Statistics and parameter estimates of line transect ($n = 49$, Total effort 392 km) based distance sampling for prey species in the Southern core of Similipal Tiger Reserve, 2021. [SE] =Standard Error.

Species	Best Model	Chi square px2	No. of observations (n)	Effective strip Width (ESW) [SE]	Encounter rate (n/l) [%CV]	Detection probability [SE]	Cluster size density [SE]	Mean Cluster Size [SE]	Density [SE]
Chital	Hazard cosine	0.912	58	29.28 [3.88]	0.14 [19.66]	0.33 [0.04]	2.52 [0.59]	5.44 [0.45]	13.76 [3.45]
Sambar	Hazard cosine	0.971	99	25.35 [2.18]	0.25 [14.32]	0.39 [0.03]	2.75 [0.20]	4.98 [0.83]	13.70 [2.50]
Northern Red Muntjac	Hazard rate Simple Polynomial	0.902	128	18.41 [1.59]	0.32 [10.64]	0.19 [0.01]	8.86 [1.21]	1.09 [0.019]	9.66 [1.33]
Hanuman Langur	Hazard cosine	0.875	78	25.31 [2.79]	0.19 [15.86]	0.34 [0.03]	3.93 [0.75]	5.73 [0.50]	22.52 [4.78]
Wild Pig	Half-normal cosine	0.889	29	31.31 [5.72]	0.07 [19.66]	0.86 [0.05]	1.18 [0.31]	5.22 [0.90]	6.16 [1.97]

Table 2.6. Model Statistics and parameter estimates of line transect ($n = 63$, Total effort 489 km) based distance sampling for prey species in the buffer of Similipal Tiger Reserve, 2021. [SE] =Standard Error.

Species	Best Model	Chi square px2	No. of observations (n)	Effective strip Width (ESW) [SE]	Encounter rate (n/l) [%CV]	Detection probability [SE]	Cluster size density [SE]	Mean Cluster Size [SE]	Density [SE]
Chital	-	-	2	-	-	-	-	-	-
Sambar	-	-	3	-	-	-	-	-	-
Northern Red Muntjac	Uniform cosine	0.849	31	22.89 [5.54]	0.06 [21.30]	0.46 [0.11]	1.38 [0.44]	1.18 [0.067]	1.63 [0.53]
Hanuman Langur	Hazard Simple Polynomial	0.609	49	28.89 [3.17]	0.10 [18.21]	0.57 [0.06]	1.73 [0.73]	5.69 [0.63]	9.87 [2.36]
Wild Pig	Half-normal cosine	0.860	16	33.17 [7.18]	0.03 [23.44]	0.70 [0.15]	0.49 [0.15]	2.27 [0.51]	1.12 [0.43]

Table 2.7. Model Statistics and parameter estimates of line transect ($n = 158$, Total effort 1243 km)

based distance sampling for prey species in Similipal Tiger Reserve, 2021. [SE] =Standard Error.

Species	Best Model	Chi square χ^2	No. of observations (n)	Effective strip Width (ESW) [SE]	Encounter rate (n/l) [%CV]	Detection probability [SE]	Cluster size density [SE]	Mean Cluster Size [SE]	Density [SE]
Chital	Hazard rate Simple Polynomial	0.907	74	27.30 [3.19]	0.05 [19.27]	0.31 [0.03]	1.09 [0.24]	5.58 [0.39]	6.09 [1.43]
Sambar	Hazard rate Simple Polynomial	0.926	122	23.37 [2.13]	0.09 [15.07]	0.36 [0.03]	2.10 [0.36]	2.55 [0.17]	5.36 [1.01]
Northern Red Muntjac	Hazard cosine	0.961	219	21.06 [1.33]	0.17 [9.49]	0.22 [0.01]	4.18 [0.47]	1.08 [0.01]	4.51 [0.51]
Hanuman Langur	Hazard rate Simple Polynomial	0.846	181	27.75 [1.65]	0.14 [10.13]	0.37 [0.02]	2.62 [0.30]	5.58 [0.31]	14.64 [1.91]
Wild Pig	Half-normal cosine	0.946	64	26.02 [2.50]	0.05 [12.71]	0.50 [0.04]	0.98 [0.15]	4.27 [0.56]	4.23 [0.87]

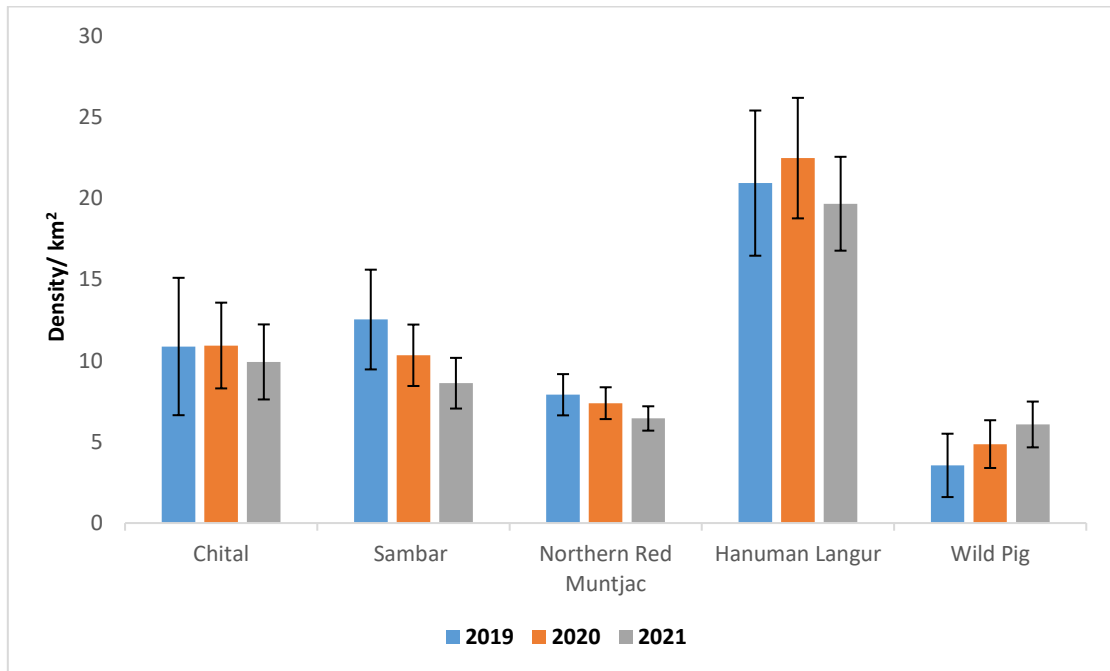


Figure 2.2. Bar graph comparing the density of major prey species in the core of Similipal Tiger Reserve.

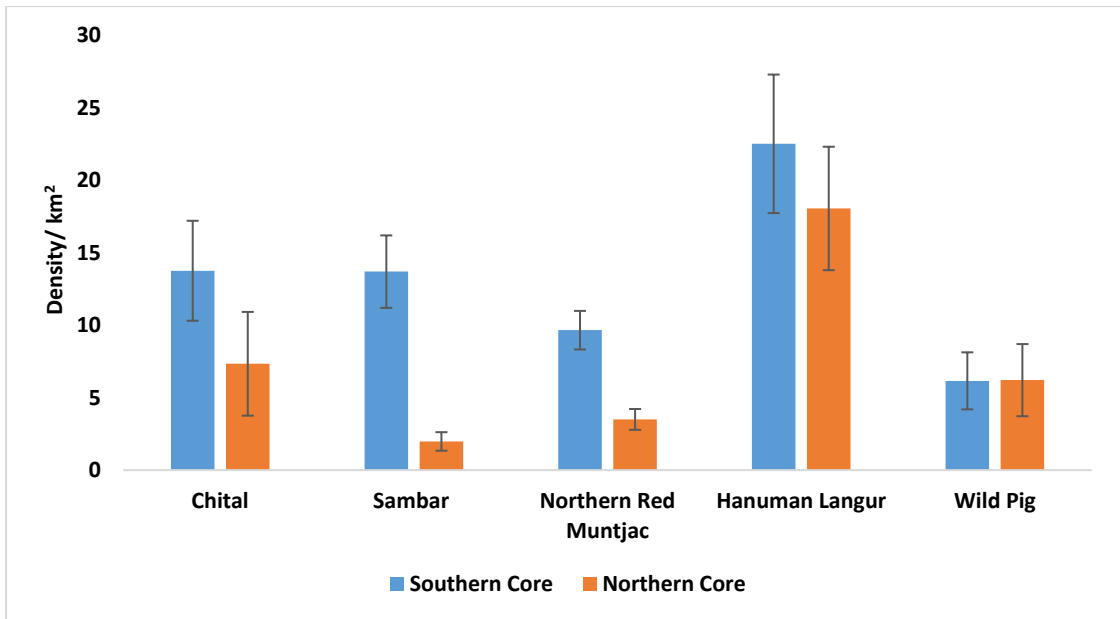


Figure 2.3. Bar graph comparing the density of major prey species in the Southern core (Bhanjabasa, UBK, Jenabil and National Park) and Northern core (Nawana South, Nawana North, Pithabata South and Chahala) of Similipal Tiger Reserve in the year 2021. The error bars are standard errors.

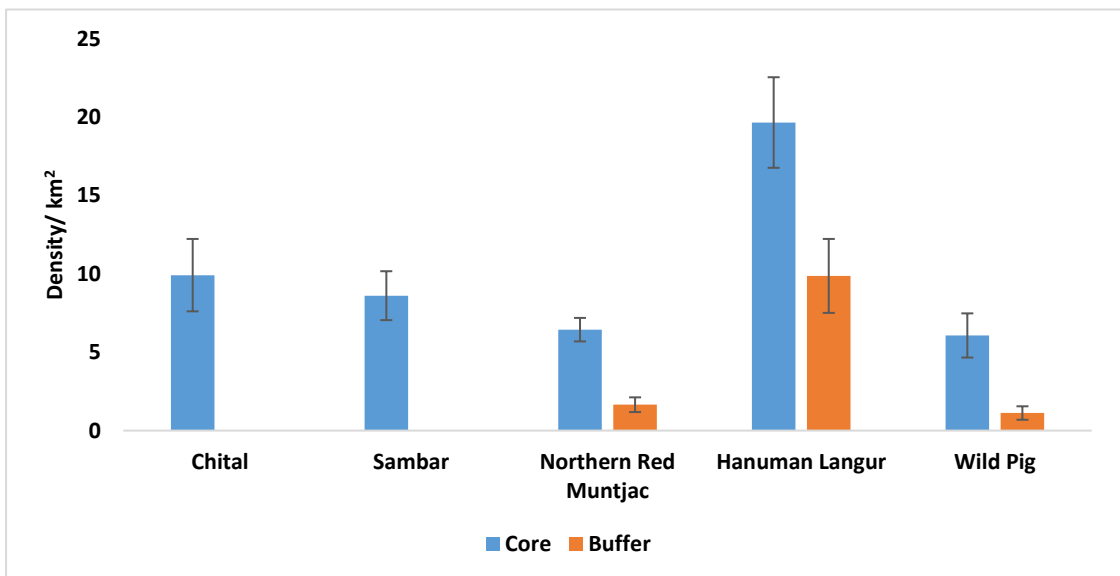


Figure 2.4. Bar graph comparing the density of major prey species in the core and buffer of Similipal Tiger Reserve in the year 2021 (Chital n=2, Sambar n=3, very low observation in buffer for suitable analysis). The error bars are standard error.

The entire core data of 2021 was subdivided into southern core and northern core. The southern core consisted of four forest ranges in the geographical south and made most of the crucial inviolate space in STR. The southern core had forest ranges that are not bordered by villages, namely UBK, Jenabil, Bhanjabasa, and National Park (exposed to villages in its northern part). The northern core lie in the geographical north and comprised of the four forest ranges lying in the vicinity of villages or bordered by them i.e. Chahala, Nawana North, Nawana South and Pithabhata South. The northern core, although surrounded by villages, is devoid of villages inside it. The subdivision was done to assess if the prey density estimates in the southern core and northern core vary, given the fact that the legal protection measures remain same in both of them.

The analysis revealed that the density of major large carnivore prey such as chital, sambar, and Northern red muntjac had significantly lower densities in the northern core than the southern core (Table 2.4 & Table 2.5; Figure 2.3). In the case of chital, the number of observations ($n = 14$) in the northern core was very low even after walking thirty-nine transects with an effort of 308 km. The chital density in the southern core after walking forty-nine transects with an effort of 392 km was estimated at $13.76 \pm 3.45 / \text{km}^2$. The sambar density in the northern core stood at $1.98 \pm 0.64 / \text{km}^2$ which is significantly lower than its density in the southern core i.e. $13.70 \pm 2.50 / \text{km}^2$. The Northern red muntjac density in the southern core was estimated at $9.66 \pm 1.33 / \text{km}^2$ which is significantly higher than its density in the northern core which stood at $3.50 \pm 0.72 / \text{km}^2$. The Hanuman langur density was similar in the northern core, i.e., $18.06 \pm 4.26 / \text{km}^2$ and southern core, i.e., $22.52 \pm$

4.78/ km². The wild pig density in the northern core and the southern core was also found to be similar and stood at $6.21 \pm 2.49/ \text{ km}^2$ and $6.16 \pm 1.97/ \text{ km}^2$ respectively. However, the number of observations of wild pigs in the northern core (n = 16) were very low to generate reliable density estimates, and care should be taken while interpreting the results.

A separate analysis for comparing the density of prey between the core and buffer was conducted for the data collected in 2021. The analysis revealed that the density of all the major prey species was significantly low in the buffer region compared to the core (Table 2.3, Table 2.6; Figure 2.4). The large carnivore prey depletion in the buffer could be understood from the fact that the observations of chital (n = 2) and sambar (n =3) were too low to conduct density estimation analysis even after walking sixty-three transects with an effort of 489 km. The density of Northern red muntjac was estimated at $1.65 \pm 0.47/ \text{ km}^2$. The density of Hanuman langur and the wild pig was assessed to be $9.87 \pm 2.36/ \text{ km}^2$ and $1.12 \pm 0.43/ \text{ km}^2$ respectively.

Overall, one-hundred fifty-eight line transects were walked in entire the STR with an effort of 1243 km in 2021 (Table 2.7; Figure 2.5). The chital and sambar density was found similar at $6.09 \pm 1.43/ \text{ km}^2$ and $5.36 \pm 1.01/ \text{ km}^2$ respectively in entire STR. The Northern red muntjac and wild pig density were estimated at $4.51 \pm 0.51 / \text{ km}^2$ and $4.23 \pm 0.87 / \text{ km}^2$. The density of Hanuman langur in the entire STR was $14.64 \pm 1.91/ \text{ km}^2$.

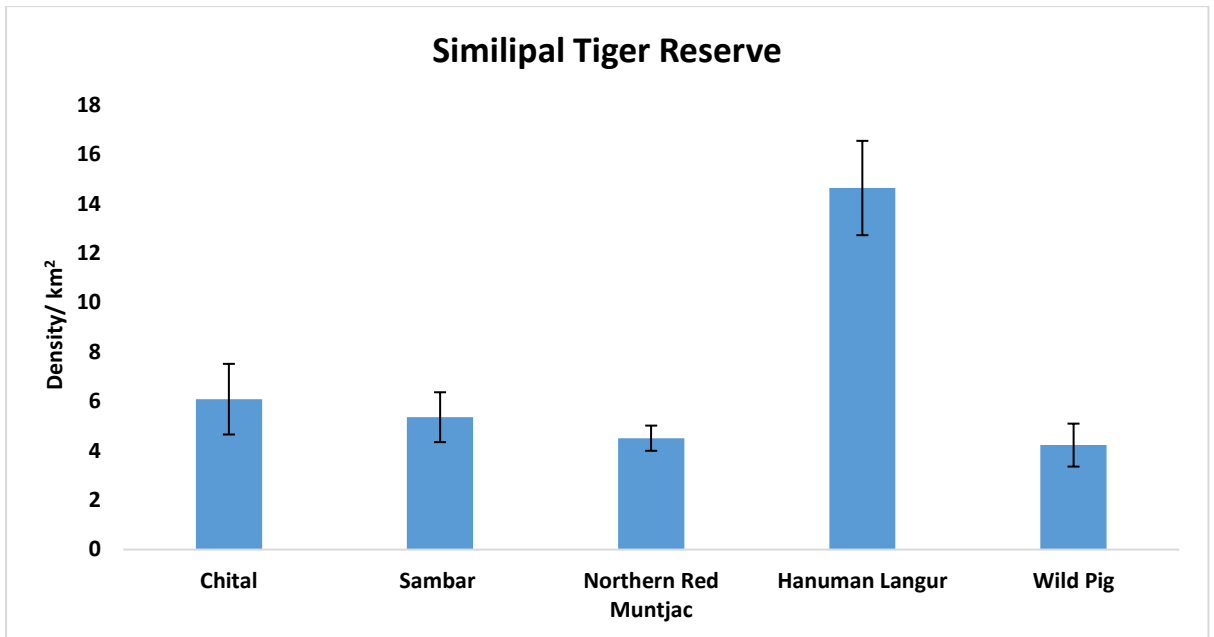


Figure 2.5. Bar graph representing the density of major prey species in entire Similipal Tiger Reserve in 2021. The error bars are standard error.

Factors governing spatial distribution of large carnivore prey in Similipal Tiger Reserve

Examination of the correlation coefficient revealed that the absolute values between each covariate were less than 0.7 (Table 2.8). This suggests that there were no statistically significant linear relationships amongst the covariates, thus precluding concerns of collinearity when incorporating them collectively into the model. Hence, all nine explanatory variables were jointly employed to construct ecologically meaningful models depicting the distribution densities of ungulate populations. The distribution pattern of chital exhibited a strong association with Normalized Difference Vegetation Index (NDVI) difference, distance to the village, and ruggedness (Table 2.9, Figure 2.6 a-c), and on the other hand; the spatial distribution of sambar (Table 2.9, Figure 2.7 a-c) and northern red muntjac (Table 2.9, Figure 2.8 a-c) was explained by NDVI difference, elevation and distance to the village. Unlike

chital, sambar, and northern red muntjac, the incorporating environmental variables did not significantly improve the model for wild pig distribution densities compared to a baseline model without these factors. Therefore, the null model was adopted for this species. Figure 2.6 a-c, Figure 2.7 a-c and Figure 2.8 a-c illustrate the geographically smoothed values of the most explanatory spatial variables employed in the model construction based on statistically significant P-values.

Corresponding to the selected statistical models used for inference i.e. (NDVI difference + Distance to village + Ruggedness) for chital, (NDVI difference + Elevation + Distance to village) for sambar, and (NDVI difference + Distance to village + Elevation) for northern red muntjac and null model for wild pig, the predicted distribution patterns of these ungulate species in space are shown in Figure 2.6 a-c, Figure 2.7 a-c and Figure 2.8 a-c respectively.

All the ungulate species were found in higher densities in the core zone of the tiger reserve than in the buffer zone. In the core zone, the chital and sambar occurred at significantly higher densities in the southern part than in the northern part. The northern red muntjac though present in reasonable densities throughout the tiger reserve also showed the high-density concentration in the southern core.

*Table 2.8. Correlation matrix depicting degree of correlation between different spatial covariates at (250m * 250m) scale.*

Covariates	Aridity	Elevation	Ruggedness	Dst_ Water	NDVI_ apr	NDVI_ nov	NDVI_ diff	Dst_Mea dow	Dst_vil
Aridity	1	-0.29	-0.04	0.06	-0.36	-0.09	0.25	0.17	-0.28
Elevation	-0.29	1	0.01	0.45	0.42	0.08	-0.32	-0.68	0.6
Ruggedness	-0.04	0.01	1	0	0.07	0.21	0.1	-0.07	-0.03
Dst_Water	0.06	0.45	0	1	0.3	0.11	-0.18	-0.49	0.32
NDVI_apr	-0.36	0.42	0.07	0.3	1	0.29	-0.68	-0.42	0.54
NDVI_nov	-0.09	0.08	0.21	0.11	0.29	1	0.51	-0.09	0.09
NDVI_diff	0.25	-0.32	0.1	-0.18	-0.68	0.51	1	0.31	-0.42
Dst_Meadow	0.17	-0.68	-0.07	-0.49	-0.42	-0.09	0.31	1	-0.49
Dst_vil	-0.28	0.6	-0.03	0.32	0.54	0.09	-0.42	-0.49	1

Table 2.9. Best DSM model among the set of candidate models for ungulates in Similipal Tiger Reserve, 2021

Species	Covariates	k`	edf	p-value	Significance level	Deviance explained (%)
Chital	s(x,y)	9	8.982	< 2e -16	***	31.7
	s(NDVI_diff)	9	7.05	< 2e -16	***	
	s(Dst_vil)	9	8.175	< 2e -16	***	
	S(Rug)	9	6.226	< 2e -16	***	
Sambar	s(x,y)	9	6.555	<2e-16	***	28.1
	s(NDVI_diff)	4	3.717	<2e-16	***	
	s(elevation)	2	1.001	0.0122	*	
	s(Dst_vil)	9	6.03	<2e-16	***	
Northern red Muntjac	s(x,y)	9	4.159	0.01423	*	7.67
	s(NDVI_diff)	4	2.438	0.02965	*	
	s(Dst_vil)	4	1.001	0.00505	**	
	s(elevation)	4	1.001	0.00546	**	

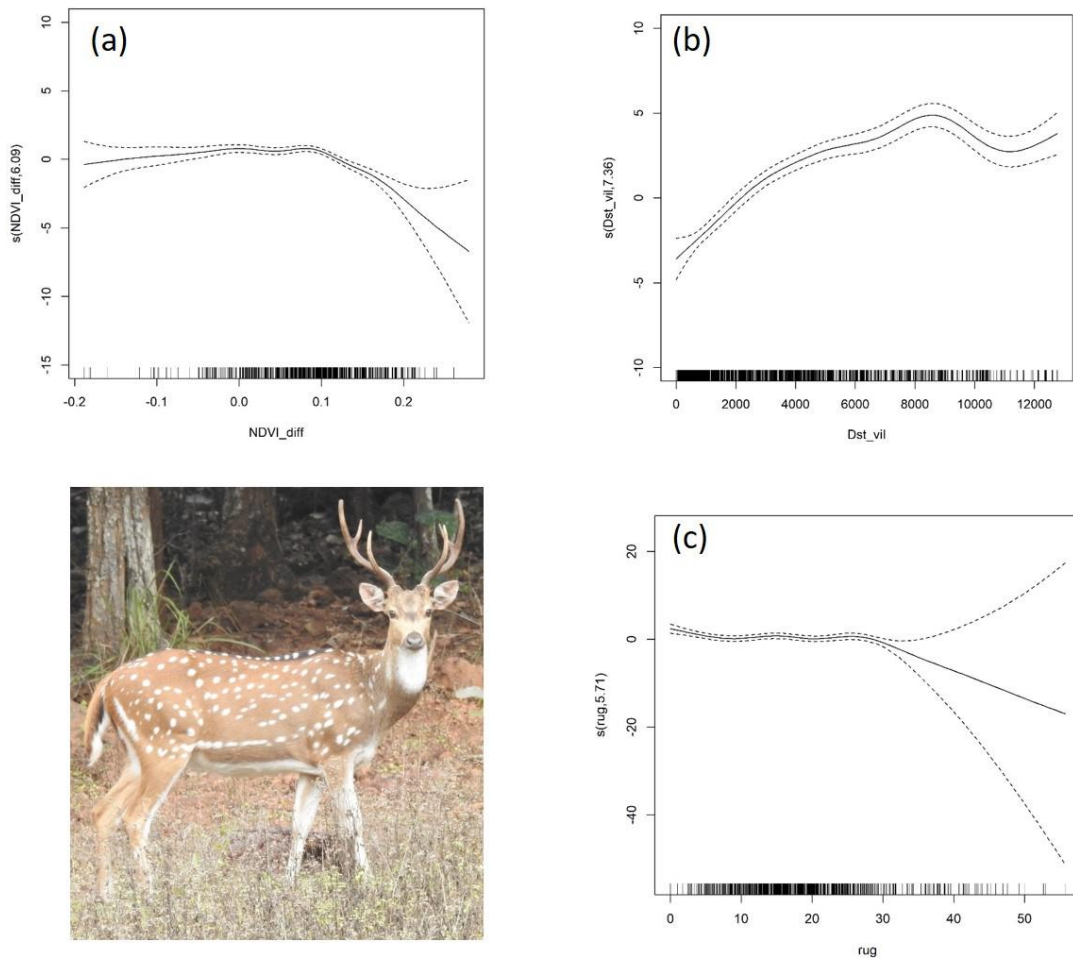


Figure 2.6. Shape of the functional forms of smooth spatial covariates with the DSM (a) NDVI difference (b) Distance to village (c) Terrain ruggedness of Chital in Similipal Tiger Reserve.

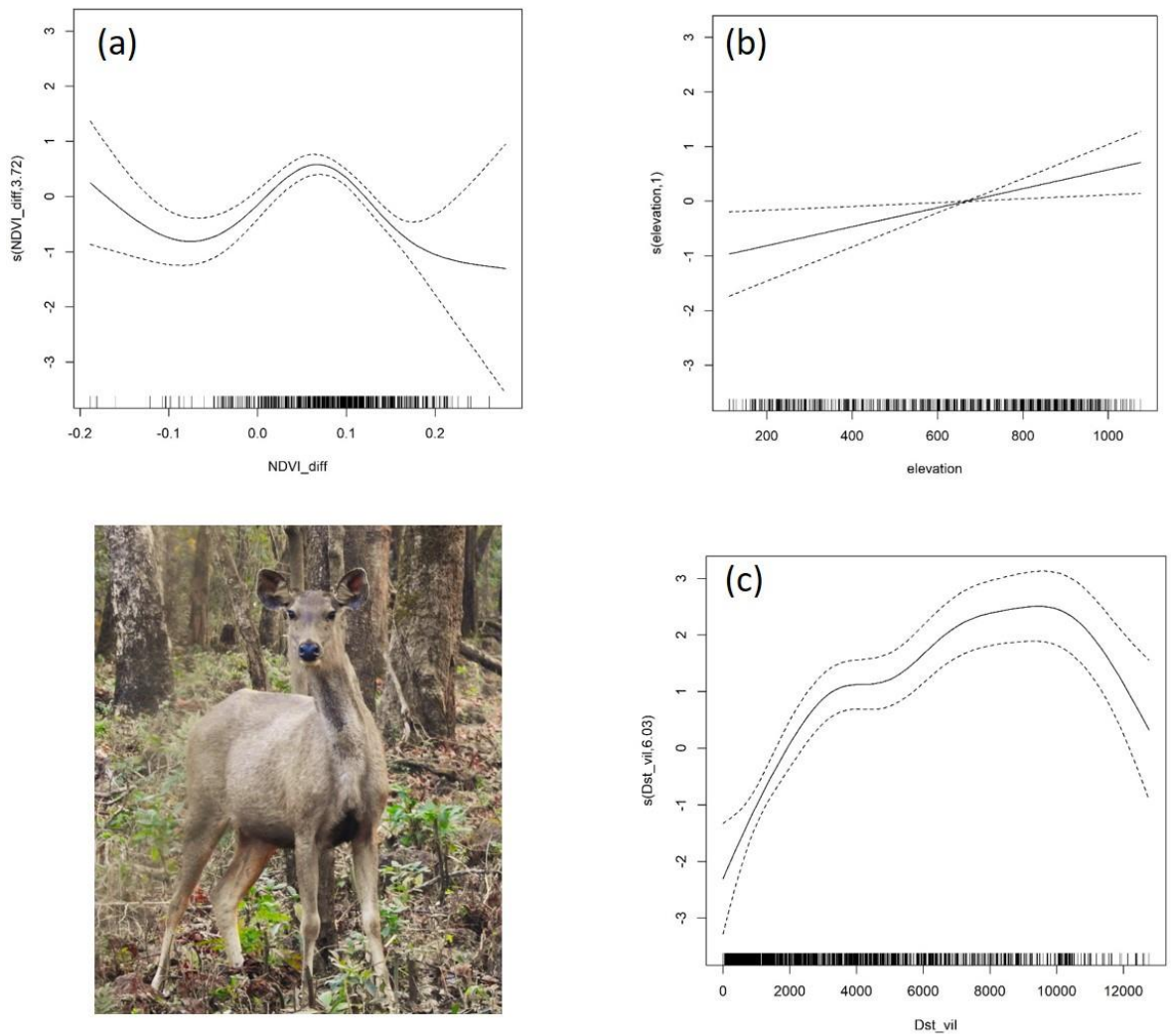


Figure 2.7. Shape of the functional forms of smooth spatial covariates with the DSM (a) NDVI difference (b) Elevation (c) Distance to village of Sambar in Similipal Tiger Reserve.

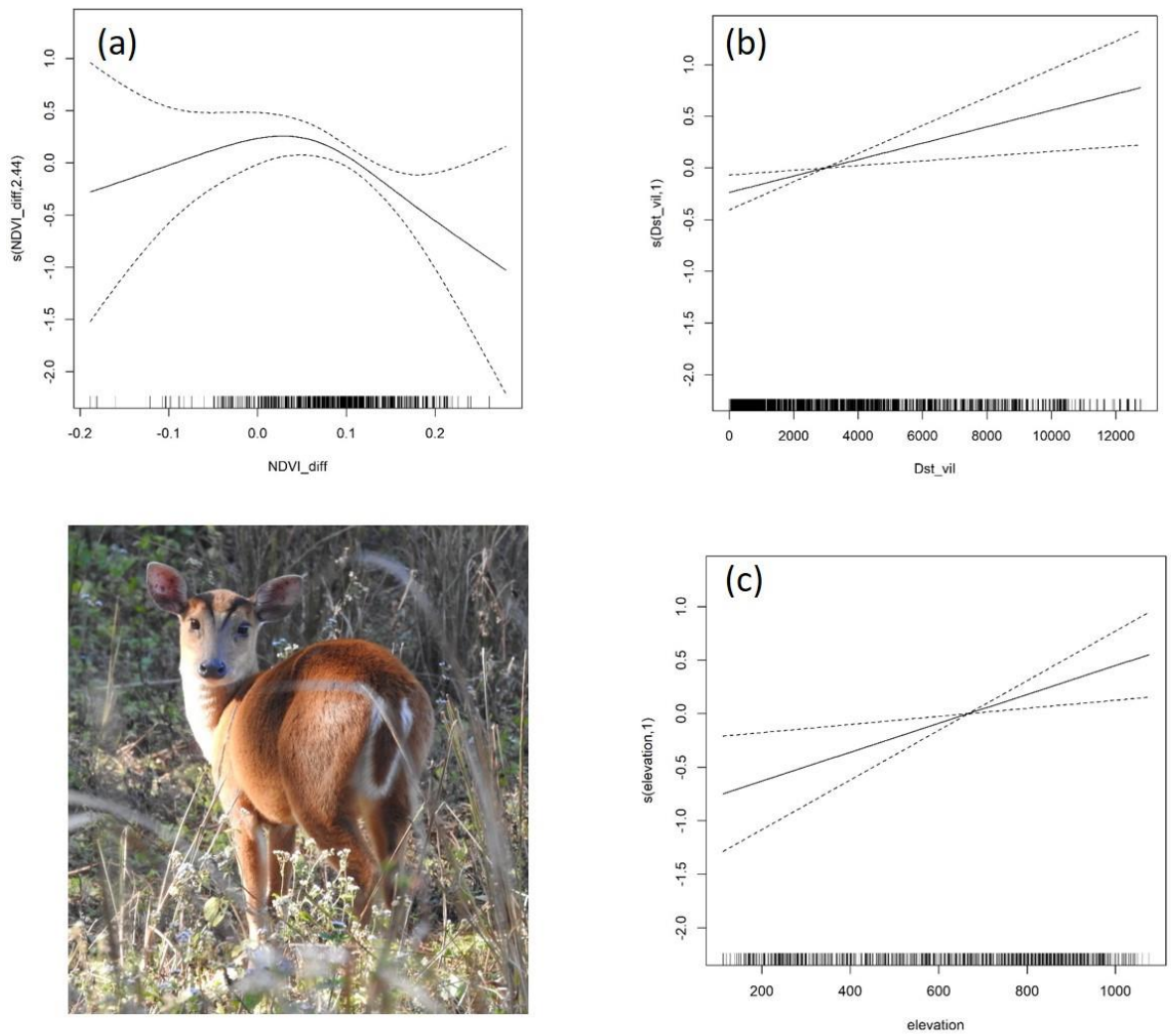


Figure 2.8. Shape of the functional forms of smooth spatial covariates with the DSM (a) NDVI difference (b) Distance to village (c) Elevation of Northern red Muntjac in Similipal Tiger Reserve.

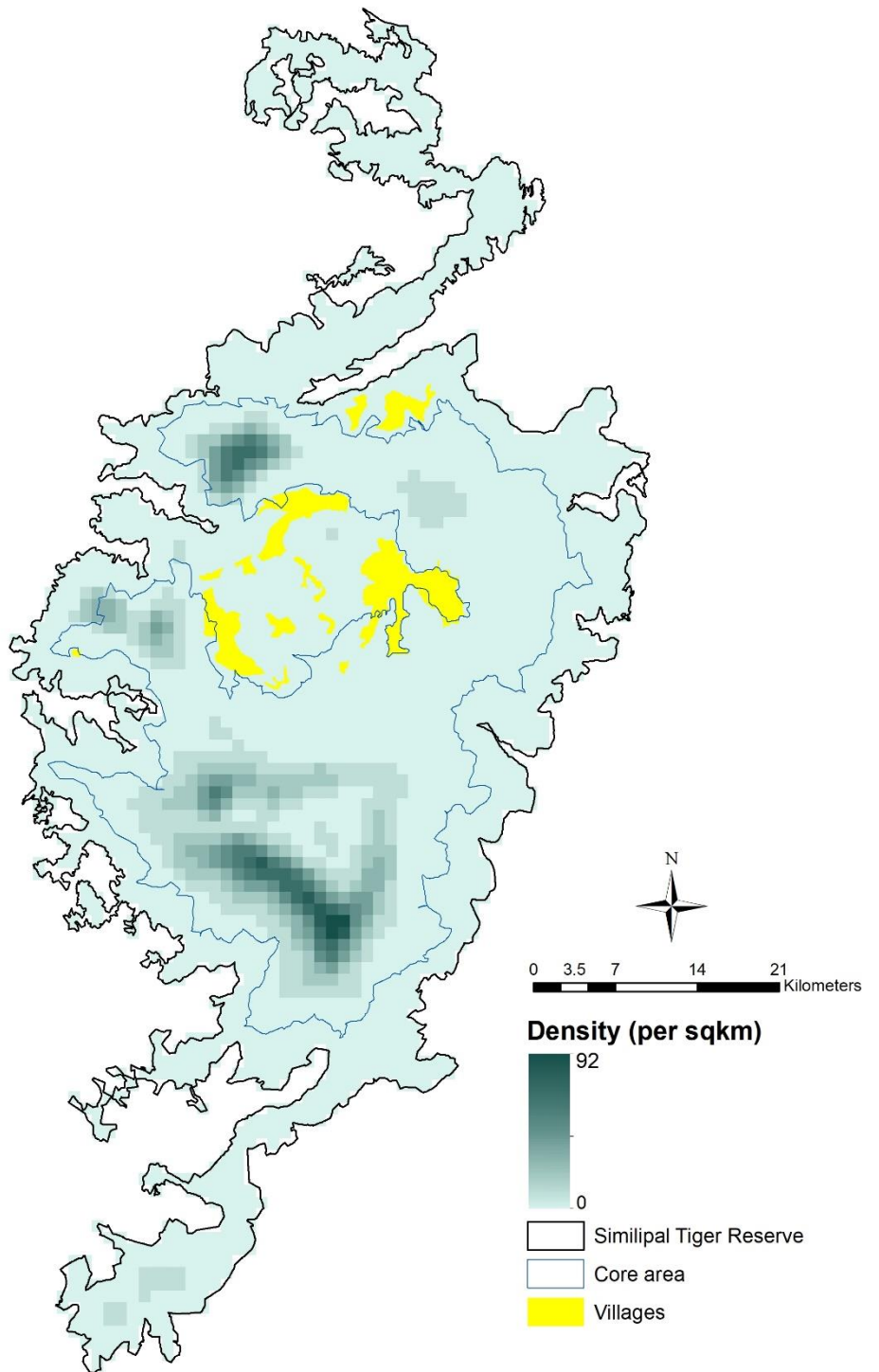


Figure 2.9. Density surface map of Chital in Similipal Tiger Reserve in 2021.

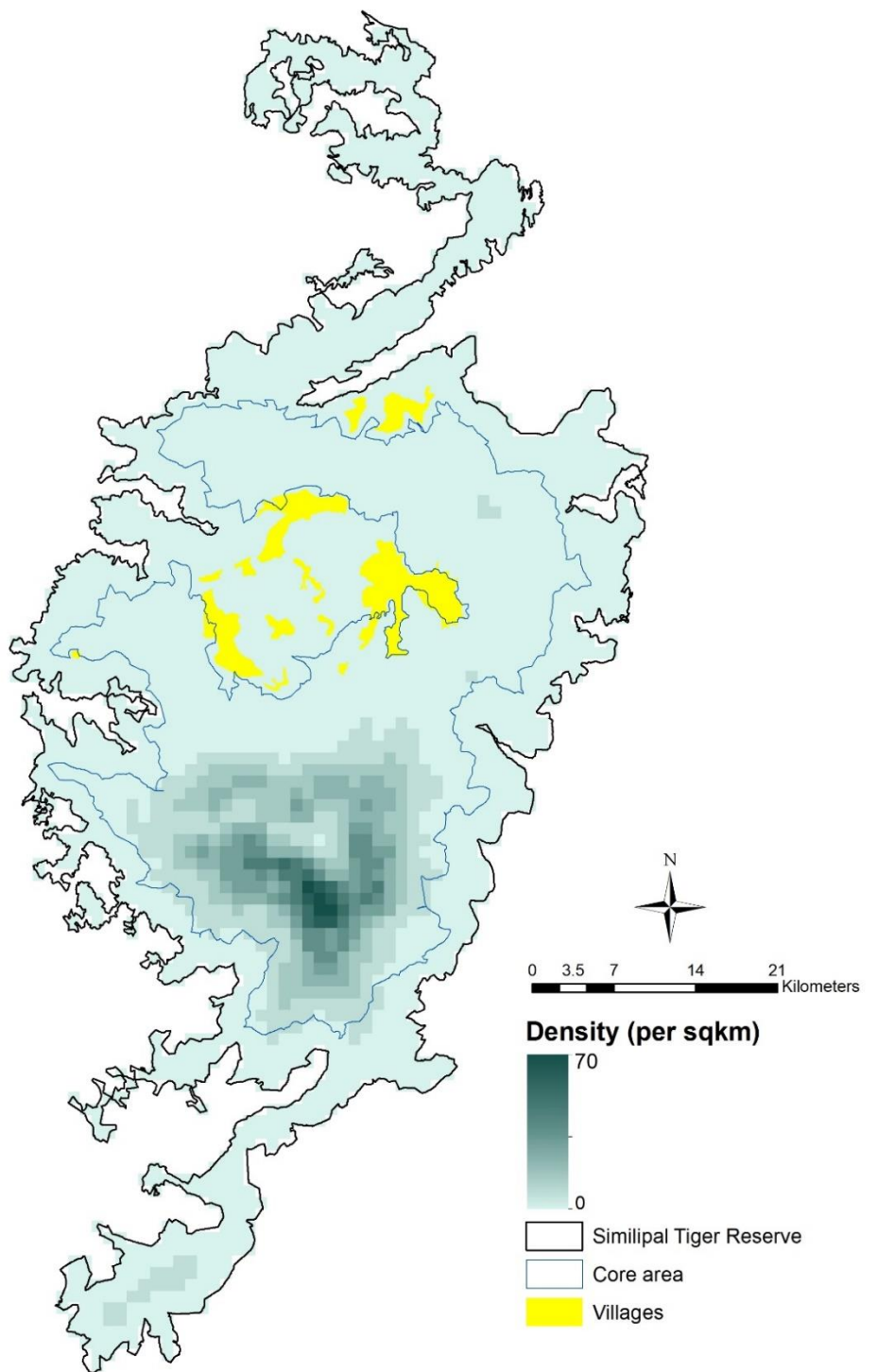


Figure 2.10. Density surface map of Sambar in Similipal Tiger Reserve in 2021.

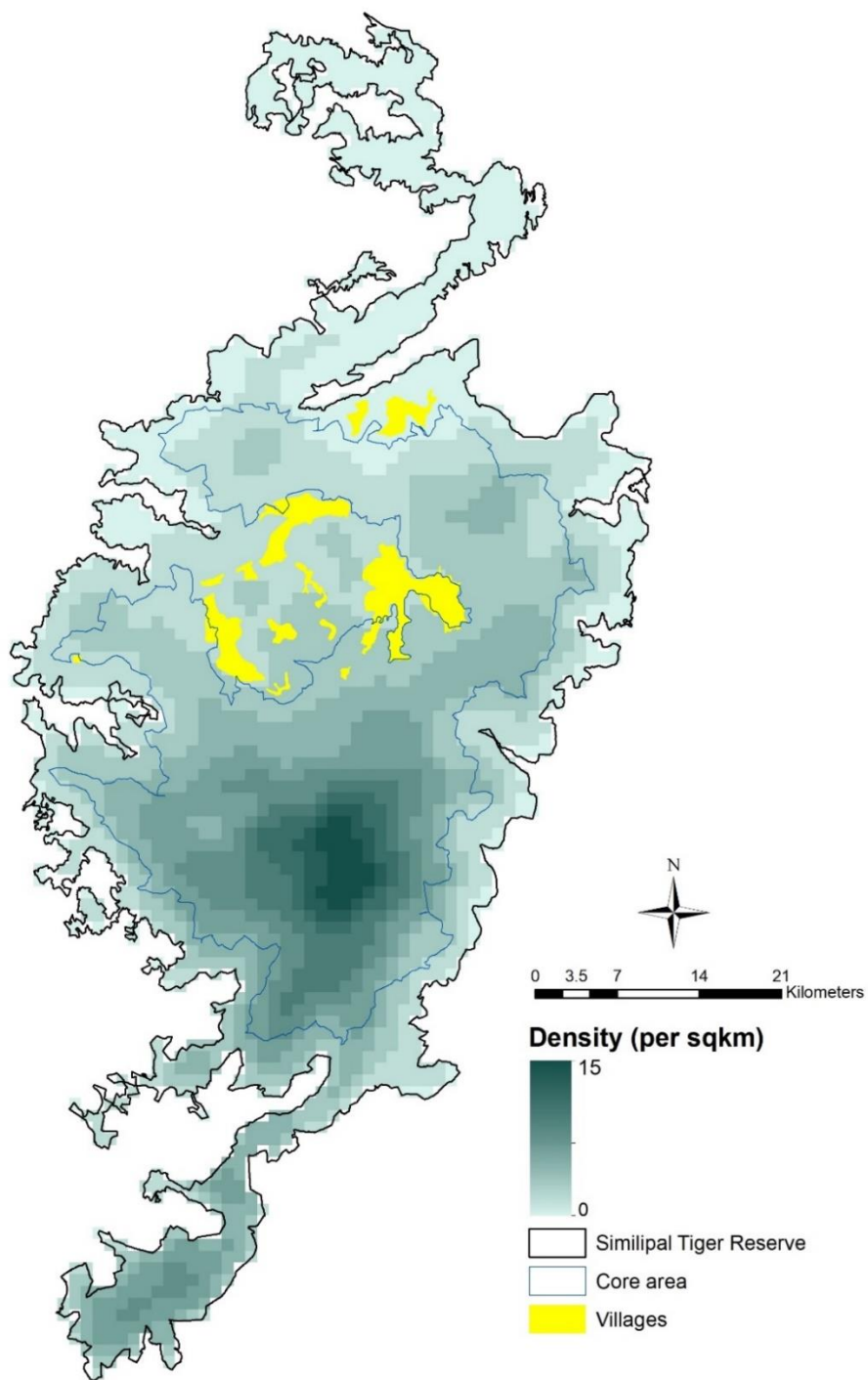


Figure 2.11. Density surface map of Northern red Muntjac in Similipal Tiger Reserve in 2021.

Discussion

The monitoring and generation of density estimates of ungulates is a challenging exercise but is crucial for the preparation of a management plan and its successful implementation (Valente *et al.*, 2016). The high density of large ungulate prey and protection from poaching are the two most critical factors that positively influence tiger recovery efforts globally (Karanth & Stith, 1999; Chapron *et al.*, 2008). This study assessed the density of all the major prey species in the core of STR to remain similar from 2019-2021. The chital and sambar densities were moderate throughout the study period. However, separate analysis for the southern core ranges and northern core ranges revealed that the densities of chital, sambar, and northern red muntjac were significantly lower in northern core than in the southern core. Moreover, the density of all the major prey species was very low in the buffer region (< 5 ungulates/ km^2) when compared to the core (~ 30 ungulates/ km^2). The buffer region forms fifty-six percent of STR's geographical area and is almost devoid of large ungulate prey. The current stronghold of tigers in STR, i.e., the southern core (**please refer to Chapter 3**), had good densities of large ungulate prey. The findings suggest that prey recovery and protection efforts are needed for the entire STR, with the focus being on the northern core and the buffer region if more tigers are to be accommodated. The dietary analysis of tiger scats also corroborates the same as the sambar and chital combined formed greater than seventy percent of its diet (**please refer to Chapter 5**). The incentivized village relocation program inside STR as previously carried out (Nayak, 2014) would actively help in prey recovery by adding to the inviolate space and reducing people's negative influence in STR.

The study revealed that NDVI difference, distance to villages, and terrain ruggedness are the major variables governing the spatial disturbance of chital in STR. Chital is an ungulate of open areas and avoids dense vegetation and rugged terrain (Mishra, 1982; Mishra & Wemmer, 1987). In Similipal, the open to moderately dense forests had no effect on chital distribution, whereas a further increase in vegetation density led to a decline in their densities. Distance to villages was another variable influencing the spatial distribution of chital. The chital densities and distance to villages were found to be negatively correlated, and high chital density regions were found to have increasing distances from villages. Thus, chital densities were mostly concentrated in the southern part of the core region (Figure 2.3 & Figure 2.7) as it was further away from the villages. They were found in very low densities in the buffer zone, as it is surrounded by the villages situated near the reserve boundary. Moreover, the northern core recorded low chital densities compared (Figure 2.3) to the southern core as most of the forest ranges here are relatively nearer to the villages located inside the reserve in the buffer zone. Chital were distributed evenly across the flat to gentle slopes region in Similipal. However, a sudden drop in their densities occurs above a certain value of terrain ruggedness.

The distribution of sambar deer in Similipal was better explained by NDVI difference, elevation and distance to villages. Sambar is typical forest-dwelling ungulate, seeking refuge within the vegetation cover during the daylight hours and emerge for foraging in the twilight and nocturnal periods (Prater, 1965; Schaller, 1967). In Similipal, the highest density of sambar was found in dense forests. However, the open and very dense forests were areas with relatively lower densities. The sambar densities were

found to be positively correlated with elevation. The observed pattern may be due to the fact that a greater part of the well-protected core zone lies 650 metres above sea level. Similar to chital, the distance to the village and sambar densities were negatively correlated for similar reasons. The southern core had the highest sambar densities and the northern core along with the buffer zone of STR had relatively very low densities.

The northern red muntjac exhibits a preference for dense habitats that conceals it from predators and humans (Wood, 1931; Powell, 1964). In Similipal, the northern red muntjacs were found in higher densities in dense forests when compared to the open and very dense habitats. They were found throughout Similipal, with the highest concentrations situated in the southern core. However, they were distributed in moderate densities in the northern core as well as the buffer region. Muntjacs are sensitive to anthropogenic disturbances; however, due to their adaptable nature and relatively small home-ranges, they manage to thrive in close proximity to the villages where the larger cervids like the chital and sambar have been extirpated (Sankar & Goyal, 2004). They were also found to be present in higher densities with increasing elevation, possibly due to the same reason described in the above-mentioned text for the sambar.

Large carnivores may suffer precipitous declines and local extinctions in regions with inadequate prey biomass (Wolf & Ripple, 2016). Similipal is a vast, isolated protected area, and its large carnivore population (particularly tiger) recruitment is largely governed by births. Thus, accommodating more tigers in Similipal is must to establish a viable population and diminish the ill impacts of the threats inherent to small

populations (Caughley, 1994; Gopal *et al.*, 2010). It has been observed that the high prey density regions support greater tiger populations, such as in Corbett Tiger Reserve and Kaziranga Tiger Reserve (Jhala *et al.*, 2015; Qureshi *et al.*, 2023). However, this study shows that distance to the village (an index of anthropogenic disturbance) impacts the densities of the major prey species in Similipal. The local community around Similipal is also involved in bush meat hunting (Nayak, 2014). Thus, it may severely impact the population growth of prey species in Similipal which has good densities only in the region (southern core) farther from the villages. It would be crucial to plan voluntary village relocation program in the buffer region of Similipal to create more inviolate space devoid of anthropogenic disturbances. The voluntary village relocations may lead to prey recovery and assist in accommodating home ranges of 20-25 breeding females in Similipal, which is required to establish a self-sustaining viable population of tigers (Gopal *et al.*, 2007).



Chapter- 3

Aspects of Tiger Demography in Similipal Tiger Reserve

Introduction

The tiger is a globally endangered large felid and continues to face existential challenges due to poaching for their body parts, hunting of their prey, habitat fragmentation, and degradation resulting from changing land use systems throughout their range (Goodrich *et al.*, 2022). India has achieved a rare conservation feat by more than doubling its tiger number between 2006-2022 (Jhala *et al.*, 2008; Qureshi *et al.*, 2023). The success resulted from utilizing the tiger's charisma and top-predator status for conserving its ecosystems through the implementation of the Wildlife (Protection) Act, 1972 followed by the commencement of Project Tiger in 1973 and subsequent declaration of tiger reserves (currently fifty-five in number) (Srivastava, 1979; NTCA, 2024). These tiger reserves currently support ~80% of the country's tiger population in mere 11% of country's forest cover area (FSI, 2021; Qureshi *et al.*, 2023). However, the threats still loom over the Indian tiger population, as the country recorded the highest number of poaching-mediated confiscation of tiger body parts (Wong & Krishnaswamy, 2022). Over the past five years (2019-2023) in India, data indicates the poaching of 220 tigers. This translates to an average poaching incident every eight days (WPSI, 2023). Nevertheless, the true number of poaching events is likely higher due to the underreporting of such incidents.

Habitat fragmentation is another significant threat in a large part of India's tiger habitat, particularly within central India and the Eastern Ghats landscape (Qureshi *et*

al., 2014; Jhala *et al.*, 2020). This landscape has experienced a substantial increase in tiger abundance from 2014 to 2022, except in the east-central states of Odisha, Chhattisgarh, and Jharkhand (Jhala *et al.*, 2021; Qureshi *et al.*, 2023). The small, isolated tiger populations of this landscape currently face various ecological, demographic, and genetic challenges (Seidensticker, 2016). The tiger population in Odisha (largely restricted in STR), in particular, is of specific conservation interest as they represent a genetically unique lineage of pseudo-melanistic tigers in the wild (Singh, 1999; Kolipakam *et al.*, 2019; Sagar *et al.*, 2021). STR currently retains the largest breeding population of tigers in the entire east-central landscape (Rathore *et al.*, 2021) and has been identified as one of the forty-two source populations of tigers in Asia (Walston *et al.*, 2010). The precise estimation of the demographic parameters of wildlife populations is vital for their successful management-based conservation (Skalski *et al.*, 2010). Moreover, only a few studies have assessed the demographic parameters of a wild population of tigers (Sunquist, 1981; Smith, 1993; Kerley *et al.*, 2003; Karanth *et al.*, 2005; Duangchantrasiri *et al.*, 2016; Majumder *et al.*, 2017; Sadhu *et al.*, 2017; Bisht *et al.*, 2019; Kumar, 2019; Dutta & Krishnamurthy, 2024). The ecological significance of STR necessitates a multi-year study to monitor tiger populations and assess demographic parameters for the first time in the east-central landscape. The data would be crucial for understanding population dynamics and informing science-based conservation strategies.

Methods

Density estimation, population trend and sex-ratio of tigers in Similipal Tiger Reserve

The use of camera-traps photo captures has revolutionized the assessment of various demographic parameters for rare and cryptic felids with unique identifiable coat patterns (i.e., stripes for tigers, rosettes for leopards) (Karanth, 1995; Karanth *et al.*, 2006; Rovero & Zimmerman, 2016). I estimated the density of tigers by deploying camera traps in the entire STR following the capture-mark-recapture framework, and the strength of this method lies in its ability to accommodate the inherent limitations of detection probability (Otis *et al.*, 1978; Karanth, 1995; Karanth & Nichols, 1998). A camera-trapping survey was planned across the core zone of STR in each 2 km² grid to encompass the intensive study area. A pre-deployment landscape-level sign survey was conducted to inform camera-trap placement. The survey targeted forest roads, jungle trails, ridgelines, trail junctions, and riverbeds, looking for large felid signs such as pugmark, urine spray, feces and scrape marks (Johnsingh, 1983). During the pre-deployment survey, the GPS coordinates of all potential large felid signs were recorded and categorized based on their freshness. Sign locations were ranked from 1 (most suitable) to 5 (least suitable) based on sign type and freshness. Rank 1 locations included fresh signs indicating active tiger use. Rank 5 locations lacked any signs but offered potential movement trails. This data was then overlaid onto a STR 2 km² camera-trapping grid to select the best sites for placing camera-traps.

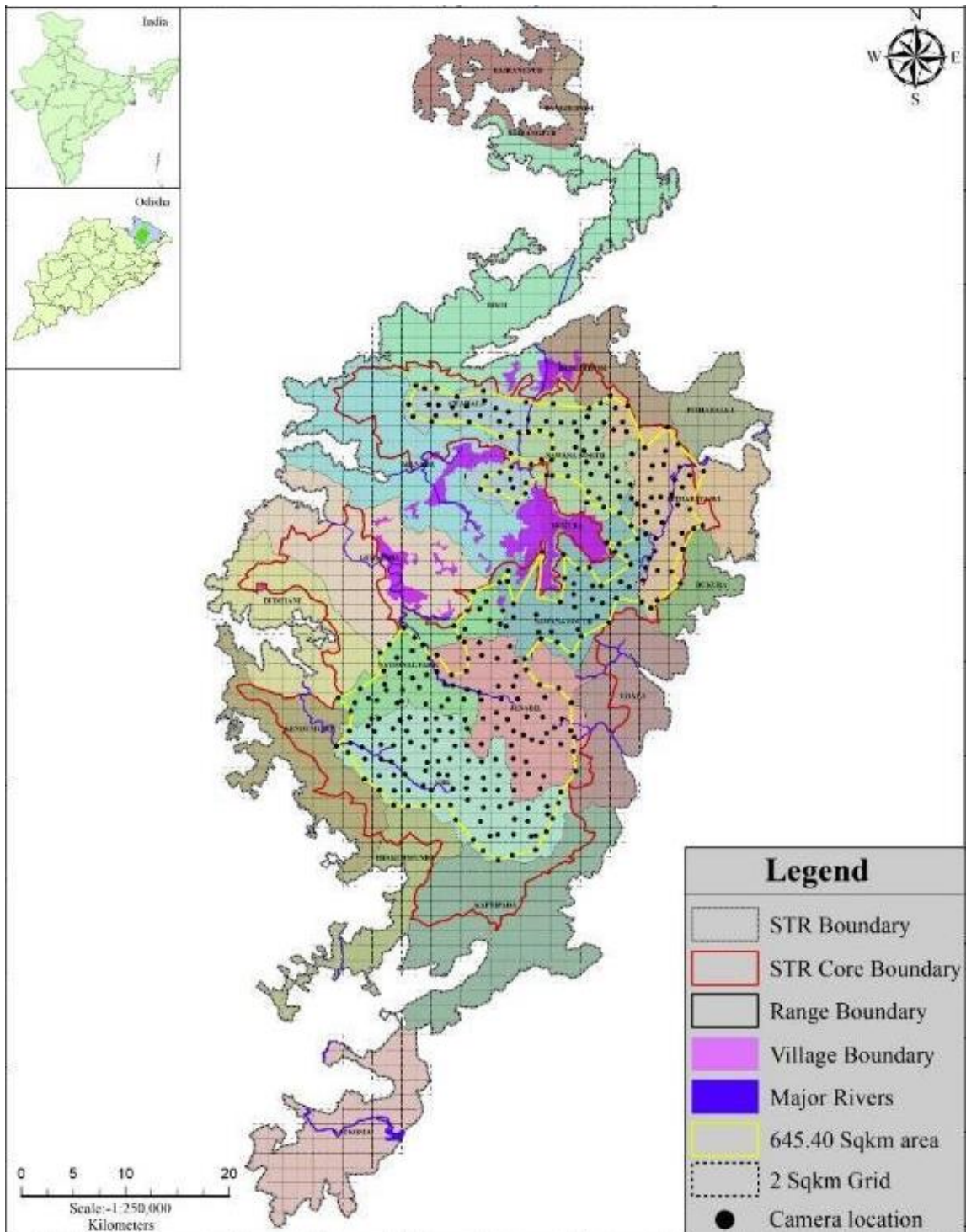


Figure 3.1. Administrative map of Similipal Tiger Reserve with the camera trap locations, 2019.

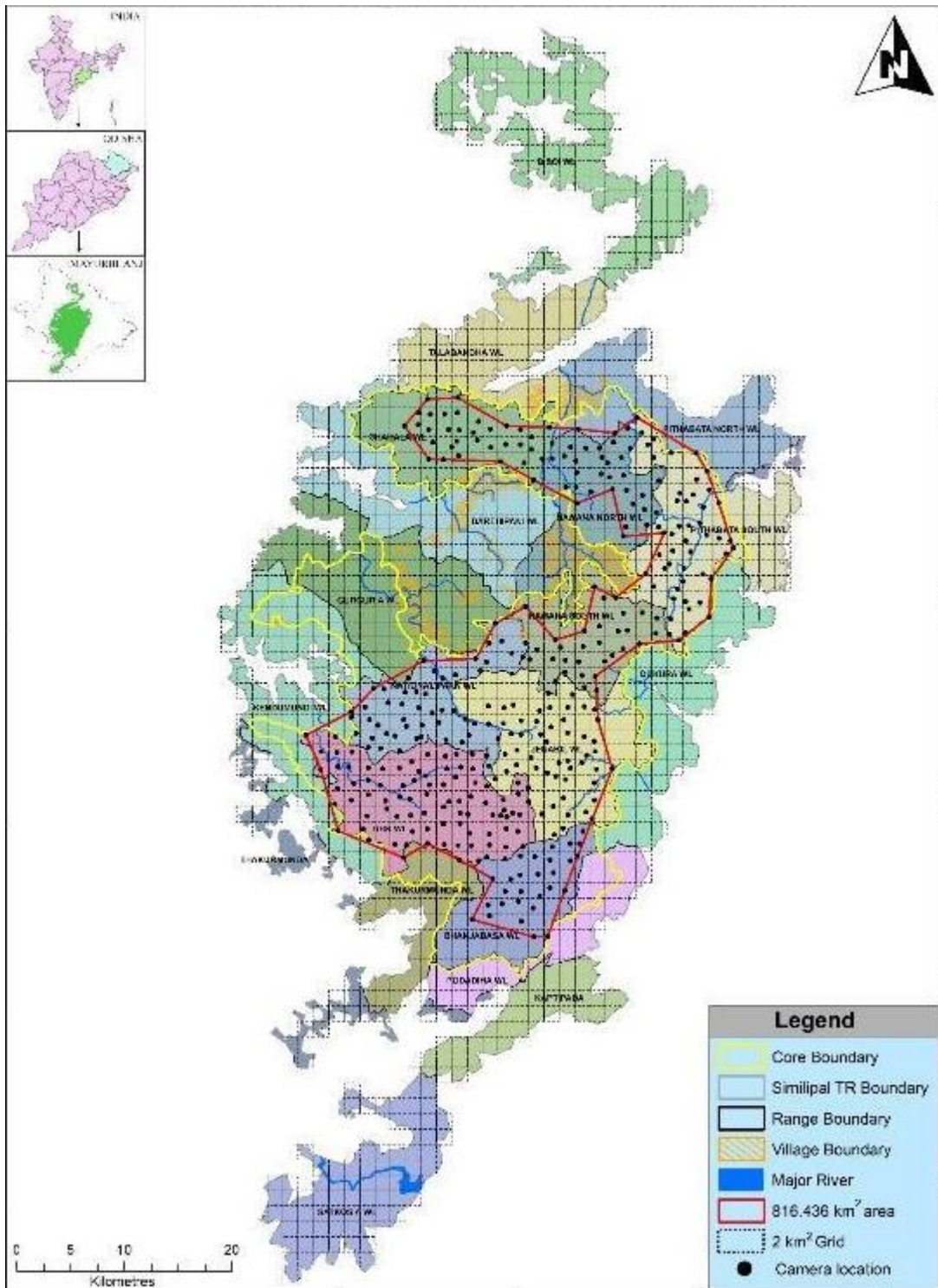


Figure 3.2. Administrative map of Similipal Tiger Reserve with the camera trap locations, 2020.

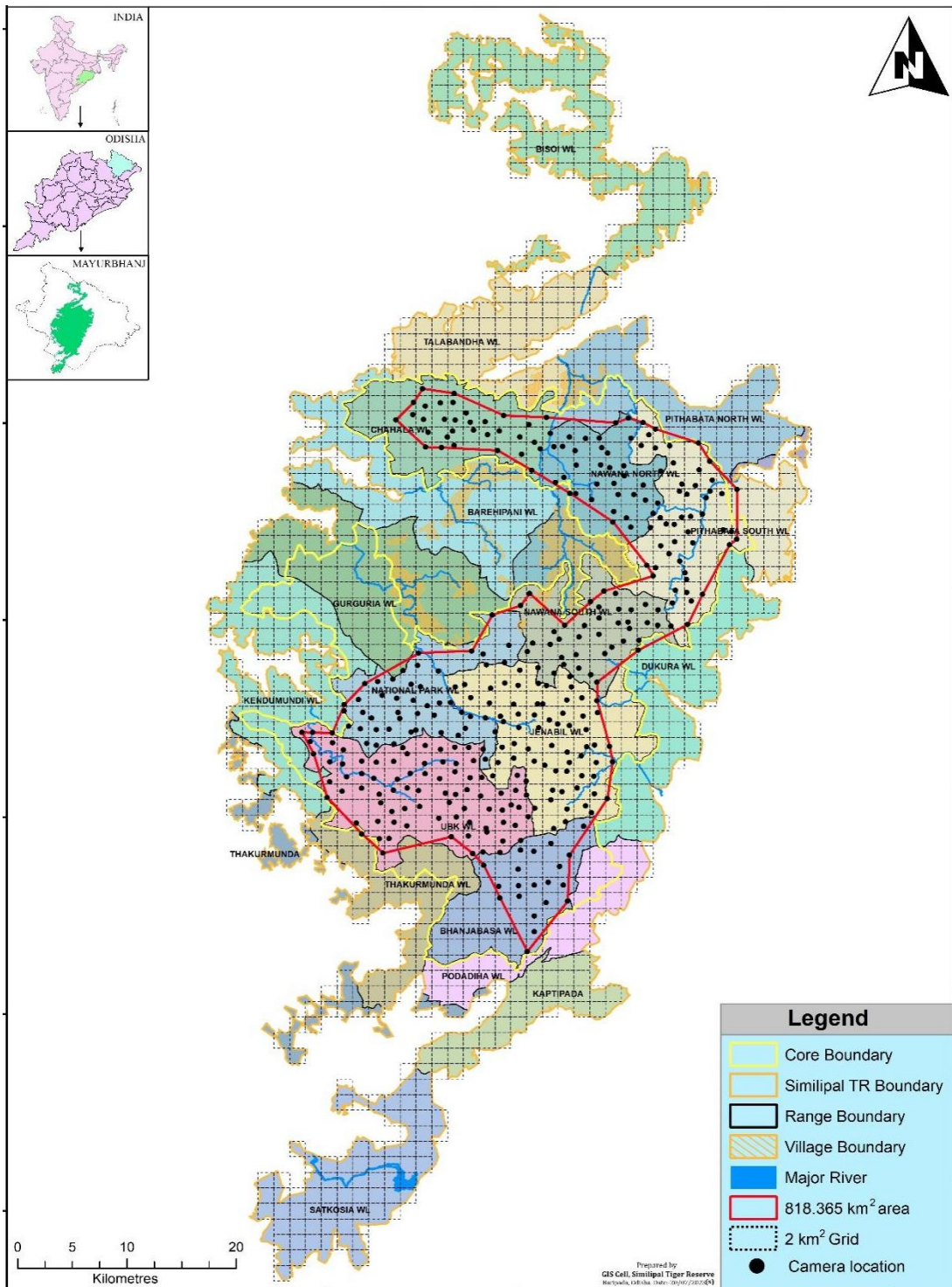


Figure 3.3. Administrative map of Similipal Tiger Reserve with the camera trap locations, 2021.

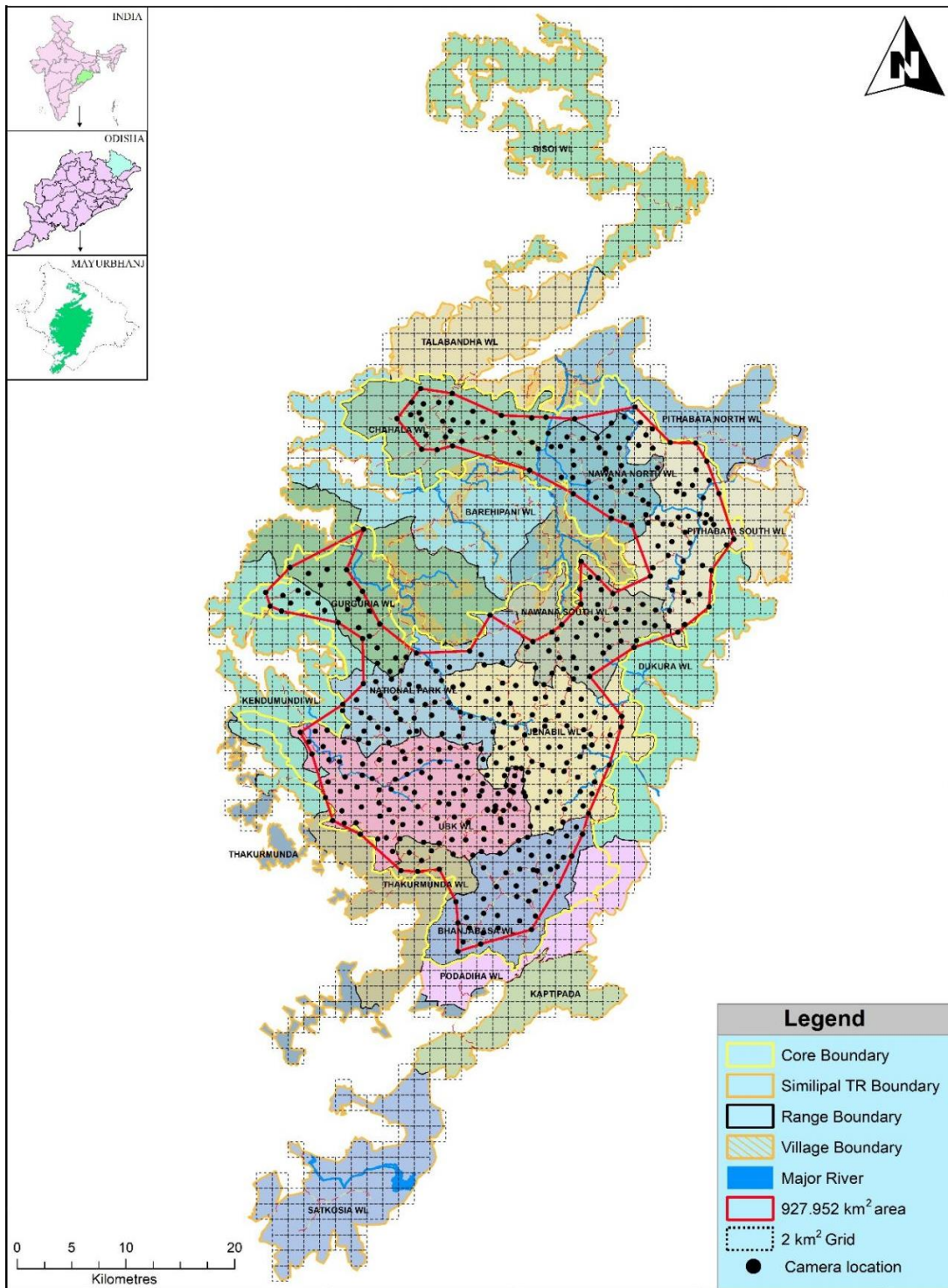


Figure 3.4. Administrative map of Similipal Tiger Reserve with the camera trap locations, 2022.

I positioned two camera traps on the opposite side of the trail at each selected site to obtain bilateral images of the large felid for individual identification. A total of 1,526 camera-trap stations were deployed across Similipal from 2019-2022, resulting in a sampling effort of 54,637 trap nights. The camera-trapping was conducted in the entire core region, with the sampled region expanding from an area of 645.40 km² in 2019 to 927.95 km² in 2022. Following data acquisition, all the tiger photographic records were meticulously sorted from the entire dataset. Each image was inscribed digitally with the date and time of capture to ensure accurate record-keeping. Subsequently, individual tiger identification was performed using EXTRACTCOMPARE (Hiby *et al.*, 2009). Finally, the capture matrix (information on animal identified, trap location and sampling occasion), trap matrix (information of spatial locations of traps, dates when particular traps were functional and sampling occasion), and habitat mask file (i.e. state-space details) were made to analyze the data in Spatially Explicit Capture-Recapture maximum likelihood framework (SECR) (Efford, 2004; Borchers & Efford, 2008).

SECR yields a much more reliable estimate for the effective trapping area than the conventional closed capture-recapture (Otis *et al.*, 1978) analysis as it utilizes the point of detection of animals to fit a spatial model of the detection process (Efford *et al.*, 2009). The two parameters involved in SECR correspond to measures of home range size (σ) and capture susceptibility (g_0). The detection process is defined by three parameters, i.e., D (density), g_0 , and σ (sigma). The basic assumption is that the detection probability decreases with the increasing distance of the detector from the home range center (Efford, 2011). In SECR analysis, the area surveyed (i.e., the area under the camera-trap array) is amalgamated with the much larger area around it,

known as the habitat mask or state space (S). It is a representation of several uniformly placed points in the form of a very fine lattice. These evenly spaced points are thought to be the potential habitat of the animals in the population being assessed. They are envisioned as potential home range centers (activity centers) of the animal being captured in the effective trapping area (ETA) (Gopaldaswamy *et al.*, 2012). These numbers of regularly spaced points were generated for this summed area using ArcGIS 9.3.

The ranging pattern of male tigers has been reported to be significantly greater than that of females (Smith, 1993; Goodrich *et al.*, 2010). The gender of individual tigers can be identified by utilizing the camera-trap images. I confirmed the gender of all the photo-captured individual tigers by examining the entire camera-trap dataset using genitalia and secondary sexual characters (mammary glands for females). To investigate the potential influence of sex on the observed variations in our data, I incorporated sex as a factor in the models for g_0 and σ . The use of hybrid mixture models in SECR (“*hcov* argument in SECR”) using the full likelihood approach accommodates the unsexed individual into a gender class based on their detection (g_0) and movement (σ) parameters. The mixing parameter indicated as *pmix* models the g_0 and σ into male and female as a two-class mixture, resulting in the detection corrected sex-ratio as a mixing proportion of sexes. The detection of corrected sex-ratio is a crucial demographic parameter concerned with population dynamics and conservation of biodiversity (Ancona *et al.*, 2017). Tiger cubs that did not reach a mid-shoulder height of their mothers (< 1year) were excluded from the analysis. This exclusion was implemented due to two key factors (1) The high

mortality rate of the young age-class (2) Movement patterns being highly dependent on their mothers (Karanth & Nichols, 1998; Jhala *et al.*, 2019).

All the models, namely $g_{0\sim 1} \sigma_{\sim 1}$ (null model), $g_{0\sim h2} \sigma_{\sim 1}$ (heterogeneity model), $g_{0\sim 1} \sigma_{\sim h2}$ (heterogeneity model) and $g_{0\sim h2} \sigma_{\sim h2}$ (heterogeneity model) were used. To achieve the most accurate density estimates for the tiger, we employed Akaike Information Criterion (AIC) based model selection approach. The model with the least AIC value was chosen as it balances model complexity and goodness-of-fit. I used the package `secr` 4.3.3. (Efford, 2024) in the R programming environment (R Core Team 2023) to generate estimates of tiger density in STR.

To estimate the tiger population trend, I regressed the natural log of the tiger population over a four-year period (2019-2022). The resulting regression slope provides the value of r (i.e., instantaneous per capita growth rate) (Caughley, 1977; Mills, 2013).

Sex-specific apparent survival of tigers in Similipal Tiger Reserve

I investigated the sex-specific apparent survival in tigers using an open-population framework. This framework allows births, immigration, deaths, and emigration within the population over the study period (Williams *et al.*, 2002; Powell & Gale, 2015). The camera-trap data for tigers captured in 2014 was obtained from Jhala *et al.*, (2015), and Odisha Forest Department provided the data for the period 2015-2018. I conducted a multi-year camera-trap study from 2019-2022, which generated another four years of data on tigers. The data from the forest department was also obtained for the year 2023, resulting in a comprehensive 10-year dataset. Given that the core sampling area remained consistent across the ten-year period, the camera-trap data

obtained from the forest department, when combined with the data collected by me, gave an opportunity to get a long-term insight into the sex-specific apparent survival of these crucial tiger populations.

To estimate the sex-specific apparent survival probability of tigers, I employed the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965; Leberon *et al.*, 1992) within a Bayesian framework (Brooks *et al.*, 2000; Kéry & Schaub, 2012). I utilized the capture history of all the adult individual tigers photo-captured during the 10-year study to arrive at the estimates. Studies that used camera-trapping commonly employ the CJS model to generate survival/mortality parameters (Karanth *et al.*, 2006; Duangchantrasiri *et al.*, 2016; Bisht *et al.*, 2019; Harihar *et al.*, 2020) for tigers. The CJS model estimates the probability of observing any specific capture history for an individual within a population. It achieves this estimation by incorporating two parameters, i.e., capture probability and survival probability. Capture probability quantifies the likelihood of an animal present during a sampling event being captured. Conversely, survival probability estimates the probability of an animal being alive during one sampling occasion and remaining alive until the next. The CJS-type analytical framework has the following assumptions: -

- (1) Each animal has equal chance of capture, p
- (2) Each animal has equal probability of surviving (ϕ . phi) to the next sampling period.
- (3) Marks are not lost/go unnoticed
- (4) Samples are instantaneous (short periods) and animals released straightaway
- (5) All emigration from the sample area is permanent

(6) Fate of animals with respect to p and φ are independent of other animals

Due to the relatively low abundance of tigers, even in the best of habitat conditions, their encounter probability with camera-traps remains limited (Karanth *et al.*, 2011). Limited camera-trap detections can lead to an inflated number of zero-capture occasions in the data. This, in turn, can pose analytical challenges and potentially lead to non-reliable estimates of survival (Gimenez *et al.*, 2003). A key framework of the Bayesian framework lies in its ability to incorporate prior knowledge about the population into the analysis alongside the collected data. This integration helps to avoid overfitting by leveraging existing information to constrain parameter estimates. Furthermore, Markov Chain Monte Carlo (MCMC) simulations employed in Bayesian analysis facilitate the assessment of parameter redundancy and unidentifiability, which can be challenging in frequentist approaches (Gimenez *et al.*, 2003; Whittington & Sawaya, 2015).

To evaluate potential variation in the parameters of interest, I compared a suite of candidate models encompassing both constant and sex-specific effects. Model selection was guided by the deviance information criterion (DIC) (Spiegelhalter, 2002), which compares the relative fit of a set of Bayesian hierarchical models. Statistical analysis were conducted using R software, version 4.3.2 (R Core Team, 2023) with the jagsUI package, version 1.5.2 (Kellner, 2021) facilitating Bayesian inference. R provided framework for the entire analysis, while JAGS (Just another Gibbs sampler) (Plummer, 2015) was employed to implement Markov Chain Monte Carlo (MCMC) methods for fitting Bayesian models. Following MCMC simulations, convergence diagnostics were employed to evaluate the mixing behavior of the Markov chains for

each model parameter. This ensured that the parameter estimates reliably reflected the posterior distribution, a crucial step for assessing the authenticity of estimates. To ensure adequate mixing of the Markov chains in the MCMC simulations, Brooks-Rubin-Gelman (BGR) statistics was employed to evaluate convergence of each model parameter utilizing the jagsUI package (Kellner *et al.*, 2021). To achieve efficient sampling from the posterior distribution, MCMC simulations were implemented using six chains, each running for 25,00,000 iterations (due to the small sample size). An initial burn-in period of 1,000 iterations was discarded to ensure convergence and eliminate the influence of starting values on the parameter estimates.

Within Bayesian analysis, the uncertainty associated with an estimate is primarily characterized by the spread of the posterior distribution. Consequently, Bayesian inference relies on the spread of the posterior high-density interval (HDI) to represent the range of plausible values for the parameter of interest rather than traditional confidence intervals (Kruschke, 2014). To evaluate potential sex-based differences in the survival parameters, I employed a two-pronged approach. First, I assessed the overlap between the posterior highest density intervals (HDIs) of the sex-specific parameter estimates. Second, I quantified the proportion of the posterior distributions for each parameter that fell within a predefined region of practical equivalence (ROPE) (Kruschke & Liddell, 2018). In instances where the posterior HDI for a parameter entirely falls outside the predefined ROPE, this provides evidence supporting sex-specific differences in the demographic parameter being analyzed.

Sex-specific recruitment of tigers in Similipal Tiger Reserve

In population ecology, recruitment signifies the process of adding individuals to a population through birth and immigration. These act as an influx, counterbalanced by the efflux of individuals through mortality and emigration. The ‘net recruitment’ of a population is a result from difference between the influx and efflux (Gaillard *et al.*, 2008). In our study, we calculated the tiger recruits (>1-year-old) recruits (B_t) in time t as;

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

where \hat{N}_{t+1} = population estimate at time $t + 1$, \hat{N}_t = population estimate at time t , S = probability of survival (Karanth *et al.*, 2006; Skalski *et al.*, 2010).

I estimated the sex-specific adult recruitment of tiger in Similipal by estimating separate male and female population from 2019-2022 using the Huggins closed capture model (Huggins, 1989; Chao & Huggins, 2005; Lukacs, 2009) through package RMark (Laake, 2013) in R programming environment (R Core Team 2023). As the camera trapping was done in multiple blocks every year due to logistics constraints, we did a combined analysis of all the blocks together for a particular year. For each block, I considered a twenty-five day period with all the camera traps functioning as the sampling period. I utilized capture histories of only those individuals who were captured during the 25 days session. The estimates generated from the combined analysis are not very different from those of each block done separately, and the gender-specific parameters derived from combined analysis are

reliable due to the increased sample size (Bisht *et al.*, 2019). I used the basic model with sex-specific detection parameters to generate robust estimates of the gender-specific tiger population and detection probabilities.

Breeding female percentage

I estimated the breeding female percentage of tigers following Bisht *et al.* (2019). I conducted a thorough analysis of the four-year camera-trap dataset (2019-2022) and identified the females with cubs and pregnant/lactating individuals as breeding (Sadhu *et al.*, 2017). Developed mammary glands with full udders are generally noticeable about 7-10 days prior to giving birth to cubs until weaning (~165 days for tigers) (Gittleman, 1986; Sadhu *et al.*, 2017). Thus, all the females that delivered cubs ≤ 5 months prior to the sampling period would be part of the breeding pool for each sampling year for estimating the detection of corrected breeding female per year. The calculation for assessing the breeding female percentage by using the below-mentioned formula:

$$\text{Breeding female per year} = (N_{Bf} / p_f) \times (D_{year} / SD_{year}) \times (D (bd) / SD_{year})$$

N_{Bf} = No of breeding female camera-trapped each year, p_f = Detection probability of breeding female, D_{year} = Number of days in a year (365 days), SD_{year} = Sampling duration (days) in each year, $D (bd)$ = Days detected as breeding (165 days).

Given that the camera-trap surveys encompassed the entire core region of the STR from 2019 to 2022, I estimated the mean annual proportion of breeding females within the population for the entire sampling duration.

Results

Density estimation, population trend and sex-ratio of tigers in Similipal Tiger Reserve

During the entire sampling duration (2019-2022), I camera-trapped 19 adult unique tigers out of which eight were pseudo-melanistic. The capture history of these unique individuals was used for subsequent analysis. In the four years, this study documented sixteen tiger cubs being born to seven different females. The sampling intensity increased over time in the study area, ranging from 11,111 (2019) to 16,079 (2022) trap nights. The number of photo captures of the tiger also increased with the progressing years. The minimum number of photo-captures occurred in 2019 ($n = 130$), while the maximum was recorded in 2022 ($n = 395$). The best fit model for estimating the density of tiger in STR was same during 2019-2021 (i.e. $g_0 \sim 1 \sigma \sim h^2$). However, in 2022, the model $g_0 \sim h^2 \sigma \sim h^2$ turned out to fit the data best. Gender was the crucial variable that explained the heterogeneity (h^2) in g_0 and σ in these models.

Table 3.1. Sampling details and tiger density parameter estimates for Similipal Tiger Reserve, 2019-2022, using spatially explicit capture mark-recapture analysis in maximum likelihood framework.

Year	Camera Location	Effort (Trap nights)	Average Trap Spacing	Unique individuals			g ₀ Male (SE)	g ₀ Female (SE)	σ Male (km) (SE)	σ Female (km) (SE)	Density/ 100 km ² (SE)
				M	F	Total					
2019	331	11111	1104.71	1	7	8	0.02 (0.003)		3.86 (0.29)	2.15 (0.12)	0.58 (0.21)
2020	365	12604	1103.04	3	9	12	0.02 (0.003)		5.24 (0.34)	2.45 (0.12)	0.75 (0.22)
2021	371	14843	1072.6	5	10	15	0.02 (0.002)		4.21 (0.30)	1.99 (0.09)	1.00 (0.26)
2022	459	16079	1042.80	5	11	16	0.02 (0.002)	0.01 (0.003)	5.02 (0.31)	2.22 (0.07)	0.89 (0.22)

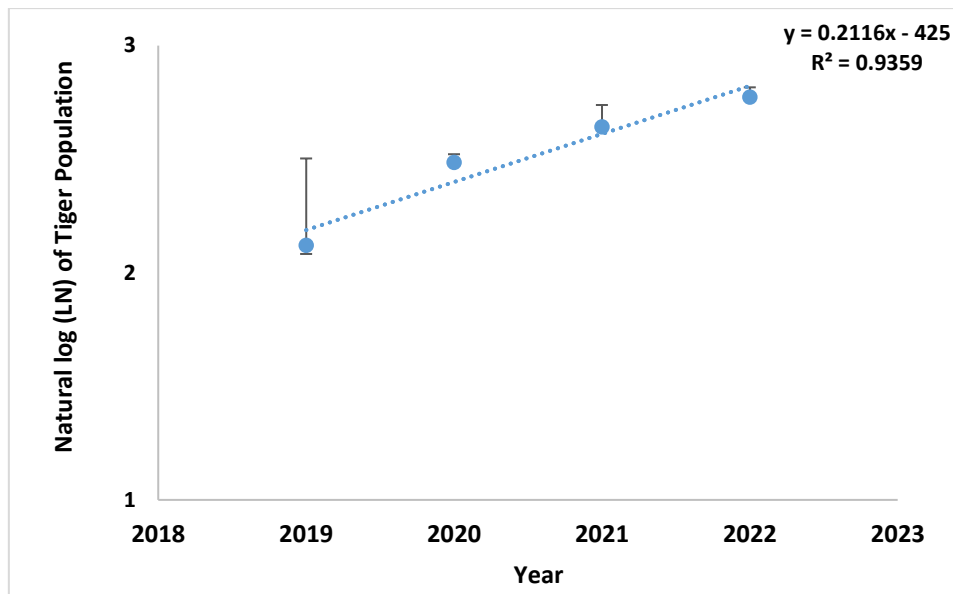


Figure 3.5. Natural log of tiger population (with 95% confidence intervals) plotted against years for 2019-2022 in Similipal Tiger Reserve

STR turned out to be a low tiger density area (Table 3.1). The tiger population in Similipal was confined to its southern core area (i.e., UBK range, National Park range, Bhanjabasa range, and Jenabil range) during the first three years of the study. In 2022, three individuals dispersed to the northern core of STR (i.e., Pithabata South WL range, Nawana South range, Nawana North range). However, the population trend points toward a significant twenty-one percent increase per annum, with a slope (r) of regression of \ln (population) against years = 0.21 ± 0.03 , $p = 0.03$, $R^2 = 0.935$ (Figure 3.5). The number of unique individuals photo-captured also doubled during the sampling duration (Table 3.1). The increase in population also led to a first-ever documentation of tiger dispersal to Kuldiha Wildlife Sanctuary through Similipal Tiger Reserve. A male tiger named T21, which was initially captured, as a cub in 2019 in Similipal, was photo-captured in December 2021 in Kuldiha Wildlife Sanctuary. However, no direct evidence of this dispersal through the Similipal-

Kuldiha corridor was obtained but the event strengthened the importance of corridor preservation in the Greater Similipal Landscape.

In 2019, we photographed eight unique individual tigers in STR. Among those captured, seven turned out to be females, and only a single male was detected. The detection corrected sex-ratio was assessed to be 0.09 ± 0.08 , which translates to 1 male: 9 females. The sex ratio for tigers in STR was extremely female-biased in 2019. In 2020, twelve individual tigers were camera-trapped in STR, out of which three were males, and the remaining nine were females. The detection corrected sex ratio was estimated at 0.33 ± 0.12 , which translates to 1 male: 3 females in 2020. In 2021, we photo-captured fifteen unique tigers, which included five males and ten females. The detection correct sex ratio was estimated at 0.49 ± 0.12 , i.e., 1 male: 2 females. In 2022, we camera-trapped sixteen individual tigers including five males and eleven females. The detection corrected sex ratio was assessed to be 0.45 ± 0.11 , i.e. 1 male: 2 females. Thus, the sex ratio of tigers in Similipal went from an extreme case of female biasness to a much normal sex-ratio in 2020 and thereafter. Thus, currently the sex ratio of tigers in Similipal is female biased in a usual manner.

Table 3.2. Details on the gender of tigers captured in Similipal Tiger Reserve along with the detection corrected sex-ratio in Similipal Tiger Reserve, 2019-2022.

Year	Unique individuals captured	Males captured	Females captured	Detection corrected Sex-ratio \pm SE	Male: Female
2019	8	1	7	0.09 ± 0.08	1:9
2020	12	3	9	0.33 ± 0.12	1:3
2021	15	5	10	0.49 ± 0.12	1:2
2022	16	5	11	0.45 ± 0.11	1:2

Sex-specific apparent survival of tigers in Similipal Tiger Reserve

In the open population analysis, the probability of encountering a specific set of capture histories depends on (i) The probability of a tiger being captured during a sampling event and (ii) the Probability of a tiger surviving between capture attempts and staying within the region. This is due to the fact that these populations are open to change continuously and undergo the processes of birth, immigration, death, and emigration. Thus, it generally becomes difficult to tease apart death from permanent emigration and the estimate generated is termed as “apparent survival” (i.e., a conservative estimate of true survival) (Karanth *et al.*, 2011). I estimated the annual apparent survival of tigers using the camera-trap dataset ranging from 2014-2023. I identified twenty-six different individual tigers during this period (12 males and 14 females). The annual apparent survival varied significantly between the genders. Male tigers had low apparent survival estimates, i.e., 0.58 (\pm 0.17 SD) indicating an average loss of ~42% of the individuals annually. The female tigers had a higher survival rate of 0.73 (\pm 0.09 SD) relative to males and reports a loss ~27% of individuals annually.

Table 3.3. Model selection table for CJS analysis of tiger data in Similipal Tiger Reserve

Models	Deviance (SE)	DIC
ϕ (~1)p(~1)	13.06 (5.09)	26.044
ϕ (~sex)p(~1)	13.07 (5.03)	25.738
ϕ (~1)p(~sex)	15 (5.37)	29.462
ϕ (~sex)p(~sex)	14.90 (5.31)	29.046

Table 3.4. Model average estimates of recapture probability (p), and annual survival (φ) from open-model Cormack–Jolly–Seber analysis based on photographic capture data.

Region	$p \pm SD$	φ Females \pm SD	φ Males \pm SD
Entire STR	0.852 ± 0.090	0.734 ± 0.096	0.582 ± 0.174

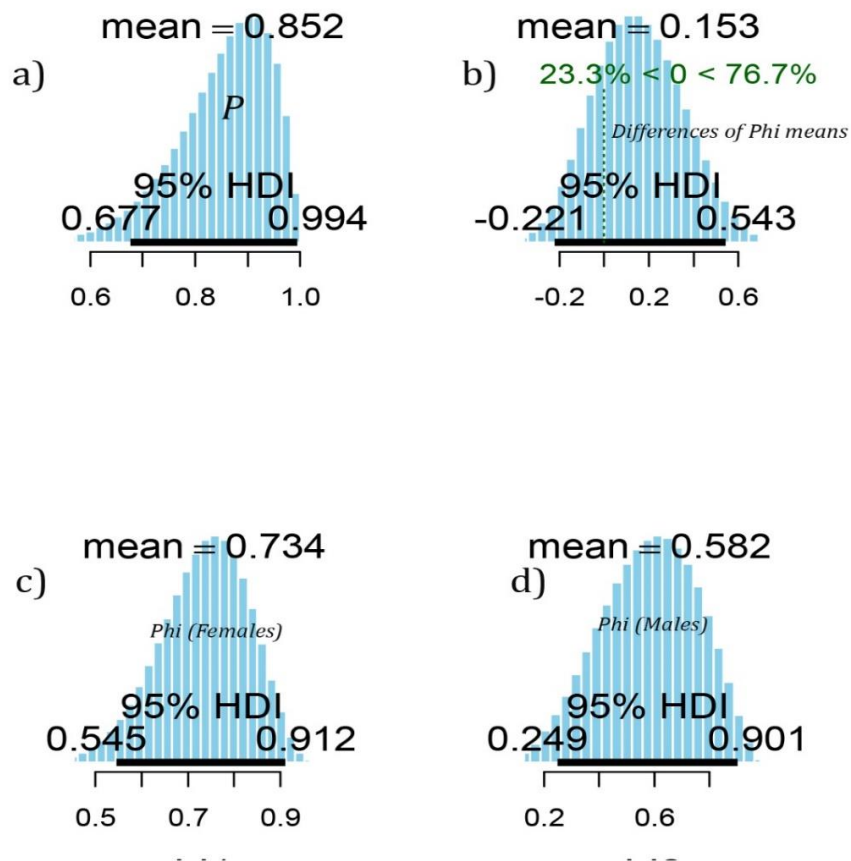


Figure 3.6. ROPE plot: sex-specific difference (tigers) in the posteriors of the survival parameters falling inside the region of practical equivalence (here the width of ROPE -1 to 1). (A) & (B) for fixed AC model (C) & (D) for Markovian AC model

Sex-specific recruitment of tigers (>1 year old) in Similipal Tiger Reserve

The mean annual recruitment of male tigers and female tigers was estimated at 2.60 (± 0.4 SE) individuals and 3.57 (± 0.8 SE) individuals respectively. Female tigers had lower recruitment percentage, i.e. 32.45% (± 8 SE), than male tigers, i.e., 52.17% (± 10 SE).

Table 3.5. Basic model (null) estimates of female tiger population \hat{N}_F , female tiger detection probability p_F , male tiger population \hat{N}_M , male tiger detection probability p_M obtained using Huggins closed-capture model from 2019-2022 along with the mean individual female/male tiger recruited annually in Similipal Tiger Reserve.

Year	M_{t+1} (F)	\hat{N}_F (SE)	p_F (SE)	M_{t+1} (M)	\hat{N}_M (SE)	p_M (SE)
2019	7	7.06 (0.26)	0.16 (0.02)	1	1 (0.002)	0.48 (0.09)
2020	9	9.01 (0.1)	0.23 (0.02)	3	3 (0.01)	0.33 (0.05)
2021	9	9.01 (0.13)	0.22 (0.02)	5	5.11 (0.36)	0.14 (0.03)
2022	11	11 (0.07)	0.26 (0.02)	5	5 (0.01)	0.33 (0.04)
Mean individual females recruited annually (SE)		3.57 (0.8)		Mean individual males recruited annually (SE)	2.60 (0.4)	

Breeding female percentage

The detection corrected mean annual breeding female percentage turned to be 42% (\pm 10 SE). This corresponds to 4 (\pm 1.05) females breeding annually in Similipal Tiger Reserve.

Discussion

Density estimation, population trend and sex-ratio of tigers in Similipal Tiger Reserve

Tigers are heavily dependent upon conservation efforts for their long-term sustenance. Thus, information on the demographic parameters of this species becomes extremely crucial to plan management actions (Sadhu *et al.*, 2017). The tigers in Similipal recorded low densities during the entire sampling duration (2019-2022). Moreover, the tigers were just confined in the southern core for the first three years. However, in 2022, three different pseudo-melanistic tigers (1 female and 2 male) were camera-trapped in the northern core. These tigers were dispersing individuals looking to carve out their own territory and were initially camera-trapped as cubs in 2020. The tigers were photo-captured urine spraying in the northern core, which is usually done to advertise one's presence to the conspecifics for demarcating their territory and by females during pro-oestrous (Smith *et al.*, 1989; Sunquist & Sunquist 2002). These records of tiger-holding territory in the northernmost region of STR in 2022 are encouraging and important if the population has to be recovered in STR. However, since the current home ranges of tigers in northern Similipal lie close to villages, the reserve officials can now expect cases of human-tiger conflict in the region. Thus, proper managerial actions targeted at protecting the tigers from poaching and

mitigating the conflict should be in place, with timely compensation to the victim of a tiger conflict being most important to reduce the probability of retaliation.

Historically, tigers were distributed throughout Similipal (Singh, 2021), but the very low density of large ungulate prey in the northern core along with the vicinity of the villages of the buffer zone could be a probable reason for their decline in northern Similipal (see Chapter 2). The density (~ 1 individual/100 km²) is on a lower scale when compared to other high-density PAs of the country. Globally, the highest tiger densities have been recorded in Indian PA's like Corbett Tiger Reserve (14.65/ 100 km² \pm 0.92 SE) and Kaziranga Tiger Reserve (13.44/ 100 km² \pm 1.32 SE) (Qureshi *et al.*, 2023). However, the tiger population has recovered in Similipal with an estimated annual growth rate of 21% (\pm 3 SE) over the four years due to the stringent management actions and strong conservation will. This might be reflected in the birth of sixteen cubs which were photo-captured during the sampling duration and, thus reaffirming Similipal as the largest recorded breeding population of tigers in the entire east-central landscape.

Over the long term, the continued recovery of tigers might further dissipate the tigers across Similipal and adjacent protected areas such as Kuldiha Wildlife Sanctuary (KWS), Hadagarh Wildlife Sanctuary (HWS) and Satkosia Tiger Reserve. The recent movement of a tiger from Similipal to Kuldiha provides a solid example of the same. The habitat and prey recovery efforts should be initiated in the protected areas of Hadagarh and Kuldiha, anticipating the arrival of more tigers in the near future and the recovery of the tiger population in Similipal. The anti-poaching patrols using (MSTripes- Jhala *et al.*, 2017) and incentivized village relocation programmes are

crucial for successful tiger repopulation in KWS and HWS. The dispersal signatures of tigers from Similipal points towards a timely intervention to protect the Similipal-Hadagarh-Kuldiha corridor. A protected Similipal-Hadagarh-Kuldiha corridor would immensely help in accommodating a few of STR's dispersing tigers in KWS and HWS if ample large ungulate prey and protected habitat are available. Similipal holds the key for the tigers to reoccupy their lost ground in the state of Odisha as well as several parts of the East Central landscape.

In 2019, one of the major concerns in Similipal was the presence of a single male and the sex-ratio being highly female-biased. The biased sex ratio of populations is a well-understood problem for the conservation of small and endangered populations (Wedekind 2002; Grayson *et al.*, 2014). In India, the population of tigers in the Western sector of Rajaji Tiger Reserve before reintroduction remained the best example of the small and isolated population being biologically and functionally extinct as just two tigresses survived a decade without a male (Harihar & Pandav 2012; Jhala *et al.*, 2015; Rathore 2015, Harihar *et al.*, 2018) and a tiger reintroduction programme had to be initiated. However, in the year 2022, we recorded five unique males in STR, thus reducing the extreme female bias in the sex-ratio of tigers. Thus, a more usual sex ratio of tigers (female-biased) (Schaller 1967, Sunquist 1981, Anile & Devillard, 2018; Bisht *et al.*, 2019; Kumar *et al.*, 2019) has been restored in 2022 in STR.

Sex-specific apparent survival of tigers in Similipal Tiger Reserve

Similipal is functionally isolated from other tiger-bearing forests (Qureshi *et al.*, 2023), and the chances of immigration are rare. However, a single adult male tiger,

which was not documented in the past camera-trap database of STR, appeared for a brief period (< 2 months) during the four years of camera-trapping (2019-2022) (Rathore *et al.*, 2021). Thus, population's growth through immigration is an exceptional chance event, and the STR tiger population is largely governed by births.

STR recorded a lower apparent survival of males, i.e., $0.58 (\pm 0.17 \text{ SD})$, than the females, $0.73 (\pm 0.09 \text{ SD})$. By analysing the raw camera-trap images and capture histories of all the tigers, it became evident that the high apparent mortality among males (mostly young) is in the period after independence from their mother till they find suitable space for establishing a territory. In the initial period (2014), STR recorded five unique individuals (4 females and 1 male) through camera-trapping in 369 km^2 area (Jhala *et al.*, 2015). Male tiger home ranges usually encompass multiple female ranges (Sunquist, 1981, Goodrich *et al.*, 2010), and the low female tiger number in 2014 could likely be monopolized by a single dominant male. The females are philopatric, and their daughters settle adjacent to their natal territories (Smith, 1993; Goodrich *et al.*, 2010; Gour *et al.*, 2013), and in due course, the female population increased (11 ± 0.07 , in 2022) (Table 3.5). The young males have to compete with dominant males or disperse to establish their territories. Infighting among males and tendencies to disperse long distances to find suitable habitats with mates an established reason for their mortality (Smith, 1993; Goodrich *et al.*, 2008), and a higher mortality rate has been recorded for sub-adult males (dispersal stage) than the adult males (breeding stage) (Robinson *et al.*, 2015). Moreover, poaching is always a threat that looms over an entire part of the tiger's distributional range in India (Wong & Krishnaswamy, 2022). Thus, the early years of male tigers after their independence till they establish territories is crucial for their survival. The primary factor governing

male territories is the access to mates (Sunquist & Sunquist, 2002) and the increasing population of female tigers in Similipal likely contributed to coexistence among males by sharing breeding partners. It also reduced the chances of dispersal outside the protected area boundary and intra-sexual strife.

The apparent survival of males (i.e., 0.6 ± 0.04 SE) and females (0.79 ± 0.05 SE) in high tiger density region of Corbett Tiger Reserve could be lower due to intense intra-specific competition between individuals (Bisht *et al.*, 2019). The apparent survival of males (0.58 ± 0.17 SD) from this study is similar to Corbett Tiger Reserve as the females might have acted as an extremely limited resource for males in this low-density population, leading to intense competition. The female apparent survival in this study, i.e., $0.73 (\pm 0.09$ SD), is lower than reported in various other studies (Sadhu *et al.*, 2017; Bisht *et al.*, 2019; Kumar, 2019) and indicates a ~ 27% loss of females annually. Chapron *et al.*, (2008) suggested that if >15% of breeding tigresses die annually, the tiger population will decline. However, with a recent 21% growth per annum in tiger population during (2019-2022), the Similipal tiger population is on a recovery trajectory.

Sex-specific recruitment of tigers (>1 year old) in Similipal Tiger Reserve

Sadhu *et al.*, (2017) recorded a higher recruitment of females to adult tiger cohort from sub-adult stage than males. However, the recruitment rate of male tigers in Similipal was significantly higher than that of females, similar to Kumar (2019), and this led the population back from the brink of functional extinction (i.e., only one sex remains). The current recruitment rates of both genders (male ~ 52%; female ~ 32%)

are greater than their apparent mortality (male ~42%; female ~27%), and hence the recorded population increase.

Breeding female percentage

The annual breeding female percentage of tigers in Similipal stands at 42% (± 10 SE), i.e., four females breeding per year. The wider confidence limits around the estimates depict high annual variability in the proportion of breeding females, and such variability is inherent to small populations. The breeding female percentage in Similipal is low when compared to other high-density areas like Corbett, which has a proportion of breeding females of more than fifty percent (Bisht *et al.*, 2019). However, Kumar (2019) in Kanha Tiger Reserve presented a close estimated figure of breeding female percentage (range 44- 53%) to Similipal. The number of breeding females in Similipal (i.e., 4 ± 1.05) is currently lower than the suggested figure of 20-25 needed for a viable population (Gopal *et al.*, 2007).

An increase in prey densities and continued stringent protection measures are needed to further boost the recovery of this genetically unique tiger population (Kolipakam *et al.*, 2019). Moreover, the earlier practiced management activities for the creation of inviolate space, primarily through voluntary village relocation programs (Nayak, 2014), would further help in prey recovery efforts and accommodating more breeding tigers in Similipal Tiger Reserve. Similipal is a vast landscape and thus has a crucial role to play for tiger conservation in the state of Odisha and the entire East Central Landscape (state of Chattisgarh, Jharkhand, Odisha put together). The tiger population has increased in STR from 2019 to 2022 due to stringent management actions and strong conservation will. Although the tiger population has increased, it is

still small, and the small populations are very much prone to demographic and environmental stochasticity (Shaffer, 1981; Soulé, 1987). In particular, large carnivores are much more vulnerable to the small population paradigm as their apex position in the ecological pyramid constrains them to exist at low population densities (Woodroff & Ginsberg, 1998). Even a small population could recover and sustain itself there is connectivity with a source population (Bisht *et al.*, 2019). The nearest tiger reserve from Similipal is Satkosia Tiger Reserve, where the tigers have become locally extinct (Qureshi *et al.*, 2023). Therefore, Similipal at present remains a small functionally isolated population, which remains a critical situation for the persistence of any population of large carnivores. Thus, continued protection efforts, along with intensive research and monitoring, are required to boost this population through the ongoing tiger conservation program in the state of Odisha.



Chapter- 4

Aspects of Leopard Demography in Similipal Tiger Reserve

Introduction

The understanding of demographic parameter estimates is central to gaining insights into the population biology of a species (Pollock *et al.*, 2012; Sandercock, 2020). Carnivores have seen a worldwide decline, and urgent efforts are needed to generate information on their demography to establish a scientific base for future conservation measures (Boitani & Powell, 2012). In reality, the demographic processes are spatially explicit and are influenced by the local ecological features and anthropogenic effects. Thus, location-specific estimates of “state variables” and “vital rates” are crucial to gain a complete understanding of the demographic process (Pollock *et al.*, 2012). The leopard is the most widely spread large felid and is globally threatened (Castello, 2020; Stein *et al.*, 2023). Its population in the Indian subcontinent has perished by 75-90% in the last 120-200 years (Bhatt *et al.*, 2020). On average, four leopards are poached every week in India (Raza *et al.*, 2012), and around 1485 leopards were poached in India in the last decade (2013-2022) (WPSI, 2023). Additionally, the interspecific interactions with other sympatric large carnivores have also been recognized to affect leopard distribution and abundance (Edgaonkar, 2008; Mondal *et al.*, 2012; Jacobson *et al.*, 2016). The targeted management and investments towards tigers can artificially inflate their densities and prove detrimental for co-predators (Kumar *et al.*, 2019), and hence, the leopard

demographic information is vital for their conservation management in these tiger-centric managed landscapes.

The information on the leopard population ecology in India is mostly limited to snapshot abundance estimates (Edgaonkar, 2008; Harihar *et al.*, 2009; Kalle *et al.*, 2011; Athreya *et al.*, 2013; Borah *et al.*, 2014; Selvan *et al.*, 2014; Jhala *et al.*, 2015; Jhala *et al.*, 2021; Qureshi *et al.*, 2024). However, few studies reporting multi-year density estimates have also been published (Kumar *et al.*, 2019; Gubbi *et al.*, 2021). The knowledge of leopard vital rates is very scarce and currently restricted to only a few studies globally (Balme *et al.*, 2009; Owen *et al.*, 2010; Swanepoel *et al.*, 2015; Rosenblatt *et al.*, 2016; Vinks *et al.*, 2021; Rostro-Garcia *et al.*, 2023). Apart from Kumar (2019), no reliable estimates of vital rates are available for the Indian leopard *Panthera pardus fusca*, which has gone extinct from seventy percent of its historic range here (i.e., higher than the species global average) (Jacobson *et al.*, 2016). Moreover, the state of Odisha, where STR is situated, has alone reported the highest number of leopard poaching-related cases (n = 20, in 2020) in India (Mendis *et al.*, 2021). Thus, it is extremely crucial to generate information on the vital rates of the leopard population in STR.

Methods

Density estimation, sex-ratio and population trend of leopard in Similipal Tiger Reserve

The capture-mark-recapture framework-based techniques using camera traps (Karanth, 1995; Karanth & Nichols, 1998) have provided a highly successive tool to estimate abundance and other demographic parameters of elusive carnivores with distinguishable pelage pattern. The leopards could be individually identified by their distinct rosette pattern (Sunquist & Sunquist, 2002) through camera-trap images. I obtained the leopard density by using camera trap pictures on a capture-mark-recapture framework (Otis *et al.*, 1978; Karanth, 1995, Karanth & Nichols, 1998). The principal advantage of the method is the aspect of taking into account imperfect detection. I conducted camera trapping in the entire core of Similipal Tiger Reserve following the national guideline of a 2 km² grid design to cover the intensive study area (WII-NTCA, 2018). A preliminary sign survey for the tiger and leopard was carried out to identify suitable sites for mounting the camera trap stations. Various signs, such as pugmarks, scats, scrapes, rakes, and urine spray, were recorded to finalize the place of camera trap installation. I deployed the cameras on both sides of the trail to capture each flank of the large felid. A Total of 1526 camera stations were installed from 2019-2022 which resulted in an effort of 54637 trap nights in the entire STR. The camera-traps remained operational continuously (24 hours per day) throughout the sampling period. Each camera-trap was deployed for a minimum of 25 days (WII-NTCA, 2018).

All the leopard photographs were sorted out from the entire data set and were digitally stamped by date and time of capture. The identification of individual leopards was carried out by using the software HotSpotter (Crall *et al.*, 2013). Finally, the data was made ready to be analysed using Spatially Explicit Capture-Recapture maximum likelihood framework (SECR) (Efford, 2004; Borchers & Efford, 2008) (**for details refer to Chapter 3**).

The male leopard and female leopard have different ranging patterns (Bailey, 1993; Sunquist & Sunquist, 2002) and the sexes can be differentiated using camera-trap images. I ascertained the gender of the leopards from the four-year camera-trap dataset by using genitalia and secondary sexual characters (nipples for females and prominent dewlap size for male leopards) (Balme *et al.*, 2012). As gender could be the potential source of variability in our data, I modeled g_0 and σ with it. I used hybrid mixture models in SECR (“hcov argument in SECR”) using a full likelihood approach to estimate detection corrected sex ratios for leopards. Sex ratios are a very crucial demographic parameter that governs various ecological processes concerned with reproductive success, risks of extinction and population dynamics (Székely *et al.*, 2014; Anile & Devillard, 2018). The leopard cubs smaller than the mid-shoulder height of their mother were excluded from the analysis due to the high mortality of this age group and their highly dependent movement patterns (Karanth *et al.*, 1998; Jhala *et al.*, 2019).

All the models, namely $g_0 \sim 1$ $\sigma \sim 1$ (null model) and various combinations of heterogeneity models (**please refer to Chapter 3**) were used. The model with the least Akaike Information Criterion (AIC) value was selected as the best-fit model to

arrive at the density estimates of leopards. I estimated the leopard density in STR by using package secr 4.3.3. (Efford, 2024) in the R programming environment (R Core Team 2023).

To assess the population trend, I analyzed capture-recapture camera-trap data collected across different years (2019-2022). Specifically, I employed multi-session models within the framework of SECR, incorporating “session” as a predictor variable to estimate the finite rate of natural increase (λ). The λ (lambda) denotes the ratio of population abundance in the subsequent year to the present year’s abundance and is calculated as below.

$$\lambda = N_{t+1} / N_t$$

where N_t is the population size at time t , and N_{t+1} is the population size a unit of time later. A population with $\lambda = 1$ is stable and is neither decreasing nor increasing. On the other hand, a population with $\lambda = 2$ indicates a doubling in abundance in a unit year, and $\lambda < 1$ signifies a decline in abundance (Mills, 2013; Sinclair *et al.*, 2006).

Sex-specific apparent survival of leopard in Similipal Tiger Reserve

I conducted the sex-specific survivorship analysis for leopards in an open population framework, i.e. time period considerable for allowing natality, immigration, mortality and emigration to occur in a population. I did it using our yearly camera-trapping exercise conducted continuously from 2019-2022. I used the “Cormack-Jolly-Seber” (CJS) method (Cormack, 1964; Jolly 1965; Seber, 1965; Leberton *et al.*, 1992) in the bayesian framework (Brooks *et al.*, 2000; Kéry & Schaub, 2012) to generate a sex-specific apparent survival probability of leopards utilizing the capture history of individually identified leopard. Many ecological studies have used the CJS model to

provide a robust framework for analyzing large-felid capture-recapture data (Duangchantrasiri *et al.*, 2016; Bisht *et al.*, 2019; Harihar *et al.*, 2020; Vinks *et al.*, 2021) (**please refer to chapter 3 for details**).

In ecological studies, the Bayesian approach for capture-recapture analysis leverages prior knowledge and advanced computational techniques to achieve precise estimates. Large carnivores like leopards and tigers usually have low detection encounters in camera-traps, which makes it difficult to generate reliable figures. The low detection in camera traps results in zero inflated data, which leads to analytical limitations and results in imprecise estimates of survivorship (Gimenez *et al.*, 2003). The major advantage of the Bayesian framework is being the integration of existing information about the population with the collected data. The Markov Chain Monte Carlo (MCMC) simulations avoid overfitting to certain parameter values for generating robust estimates and assessing parameter redundancy and un-identifiability, thus overcoming the analytical limitations (Gimenez, 2003; Whittington & Sawaya, 2015). I investigated several models for parameter variation, including models with constant effects and sex-specific effects. The model selection process employed the use of the deviance information criterion (DIC) (Spiegelhalter *et al.*, 2002). I used R software version 4.3.2 and the jagsUI package, version 1.5.2 (Kellner, 2021) for statistical analysis. The MCMC simulations were then used to assess the convergence of the model parameters, ensuring the reliability of the estimated values. Convergence of the MCMC simulations was assessed using Brooks-Rubin-Gelman (BRG) diagnostics (Brooks & Gelman, 1998) implemented within the “jagsUI” R package (Kellner, 2021). We configured the MCMC runs of six chains with 200000 iterations, discarding the initial 1000 iterations (burn-in) to improve efficiency. The \hat{R} statistic

(Spiegelhalter *et al.*, 2002) was less than 1.1, indicating the convergence of chains to a stable distribution (Kéry & Schaub, 2012).

Sex-specific recruitment of leopards in Similipal Tiger Reserve

In our study, we calculated the leopard (>1-year-old) recruits (B_t) in time t as;

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

Where \hat{N}_{t+1} = population estimate at time $t + 1$, \hat{N}_t = population estimate at time t , S = probability of survival (Karanth *et al.*, 2006; Skalski *et al.*, 2010).

A separate male and female population of leopards for the individual sampling years (2019-2022) was estimated using the Huggins closed capture model (Huggins, 1989; Chao & Huggins, 2005; Lukacs, 2009) through package RMark (Laake, 2013) in the R programming environment (R Core Team 2023). Further, I used the basic model with sex-specific detection parameters to generate robust estimates of the gender-specific leopard population and detection probabilities. *(please refer to chapter 3 for details)*

Breeding female percentage

I inspected all the female leopard photographs with great attention and assigned the “breeding” status to those who were pregnant/lactating or moving with cubs. Conspicuous nipples and full udders are generally visible about 7-10 days before parturition and till the age of weaning in large felids (~101 days for leopards) (Bailey, 1993; Sadhu *et al.*, 2017). Thus, for estimating the detection of corrected breeding

females per year, all the females that delivered cubs ≤ 3.5 months prior to the sampling period would be part of the breeding pool for each sampling year. I calculated the breeding female percentage following Bisht *et al.* (2019) using the formula mentioned below:

$$\text{Breeding female per year} = (N_{\text{Bf}} / p_{\text{f}}) \times (D_{\text{year}} / S_{\text{Dyear}}) \times (D(\text{bd}) / S_{\text{Dyear}})$$

N_{Bf} = No of breeding female camera-trapped each year, p_{f} = Detection probability of breeding female, D_{year} = Number of days in a year (365 days), S_{Dyear} = Sampling duration (days) in each year, $D(\text{bd})$ = Days detected as breeding (101 days).

As the entire core region of STR was sampled using camera-traps from 2019-2022, I estimated the mean annual breeding female percentage by pooling data for all these years.

Results

Density estimation, population trend and sex-ratio of leopard in Similipal Tiger Reserve

Over a four-year period (2019-2022), a camera-trapping effort documented 130 unique leopards. Leopards were found throughout the expanse of the study area during the entire sampling duration. The trapping intensity increased progressively across the years, ranging from 11,111 to 16,079 trap nights. Annual leopard detections through camera-trapping exhibited variation across the study period. The photo-captures used ranged from a minimum of 300 (in 2019) to a maximum of 635 (in

2022). The best-fit model for estimating the density of leopards differed across the years. In 2019 and 2021, the model structure $g_0 \sim 1 \sigma \sim h^2$ resulted in best fit, whereas in 2020 & 2022, it was $g_0 \sim h^2 \sigma \sim h^2$. The heterogeneity (h^2) in g_0 and σ in these models was explained by gender. The analysis revealed no significant variation in leopard density across the four sampling years. The leopard densities ranged from $4.99 \pm 0.65/100 \text{ km}^2$ in 2019 to $5.12 \pm 0.59/100 \text{ km}^2$ in 2022 (Table 4.1). Furthermore, the population trend suggests stability, with an estimated population growth rate λ ($\lambda = 1.01$ (CI95% 0.91-1.18)).

In 2019, we captured 60 unique individuals in the entire core of STR. Out of those 60 individuals, 16 were males, and 39 were females. We could not specify the gender of the remaining five individuals from the camera-trap pictures. The detection corrected sex ratio turned out to be 0.38 ± 0.05 , which translates to 1 male: 3 females in 2019. In 2020, we camera-trapped 63 individuals in the entire core of STR, out of which 16 were males and 42 were females. The gender of five individuals could not be specified again in 2020. The detection corrected sex ratio turned out to be 0.36 ± 0.05 , which translates to 1 male: 3 females in 2020 (Table 10). We captured 63 unique individuals in the entire core of STR in 2021, of which 19 were males and 44 were females.

Table 4.1. Sampling details and leopard density parameter estimates for Similipal Tiger Reserve, 2019-2022, using spatially explicit capture mark-recapture analysis in maximum likelihood framework.

Year	Camera Location	Effort (Trap nights)	Average Trap Spacing	Unique individuals			g ₀ Male	g ₀ Female	σ Male (in km)	σ Female (in km)	Density/ 100 km ²
				M	F	UNID					
2019	331	11111	1104.71	16	39	5	0.01 (0.001)		3.59 (0.25)	1.72 (0.08)	4.99 (0.65)
2020	365	12604	1103.04	16	42	5	0.02 (0.003)	0.01 (0.002)	3.27 (0.14)	1.47 (0.08)	5.42 (0.69)
2021	371	14843	1072.46	19	44	0	0.01 (0.001)		3.18 (0.14)	1.55 (0.07)	5.16 (0.67)
2022	459	16079	1042.80	23	53	1	0.03 (0.002)	0.01 (0.001)	3.23 (0.10)	1.76 (0.07)	5.12 (0.59)

The detection corrected sex ratio was estimated to be female-biased at 0.28 ± 0.04 , which translates to 1 male: 3 females. In 2022, a total of seventy-seven individuals were photo-captured, of which twenty-three were found to be males and fifty-three were females. One individual's gender could not be specified, and the estimated detection corrected sex-ratio was 0.42 ± 0.05 , which translates to 1 male: 2 females. Overall, the sex ratio turned out to be female-biased for leopards in a usual manner in STR from 2019-2022 (Table 4.2).

Table 4.2. Details on the gender of leopards captured in Similipal Tiger Reserve along with the detection corrected sex-ratio in Similipal Tiger Reserve, 2019-2022.

Year	Unique individuals captured	Males captured	Females captured	Unidentified gender	Detection corrected Sex-ratio ± SE	Male: Female
2019	60	16	39	5	0.38 ± 0.05	1:3
2020	63	16	42	5	0.36 ± 0.05	1:3
2021	63	19	44	0	0.28 ± 0.04	1:3
2022	77	23	53	1	0.42 ± 0.05	1:2

Sex-specific apparent survival of leopard in Similipal Tiger Reserve

The apparent survival estimates cannot distinguish between mortality and permanent emigration. Leopards with unknown genders were not subsequently captured in the next sampling period and thus were not considered for analysis. A total of 127 unique leopards (45 males; 82 females) with known genders were camera-trapped during 2019-2022, and their capture histories were used for the analysis. The probability of survival for leopards varied significantly between the genders in Similipal. Based on the lowest DIC, a model with a sex-specific effect on survivorship turned out to be the best-fit model (Table 4.3). The survival probability of male leopards was 0.630 (\pm 0.06 SD), indicating \sim 37% annual loss of the individuals. Conversely, the female leopards had a higher probability of survival, i.e., 0.802 (\pm 0.03 SD), indicating \sim 20% annual loss (Table 4.4).

Table 4.3. Model selection table for CJS analysis of leopard data in Similipal Tiger Reserve

Models	Deviance	DIC
$\phi(\sim 1)p(\sim 1)$	97.18 (18.31)	264.952
$\phi(\sim \text{sex})p(\sim 1)$	97.07 (18.04)	259.825
$\phi(\sim 1)p(\sim \text{sex})$	109.44 (20.11)	311.719
$\phi(\sim \text{sex})p(\sim \text{sex})$	102.07 (18.69)	276.83

Table 4.4. Model average estimates of recapture probability (p), and annual survival (ϕ) from open-model Cormack–Jolly–Seber analysis based on photographic capture data.

Region	$p \pm \text{SD}$	ϕ Females \pm SD	ϕ Males \pm SD
Entire STR	0.892 \pm 0.035	0.802 \pm 0.037	0.630 \pm 0.066

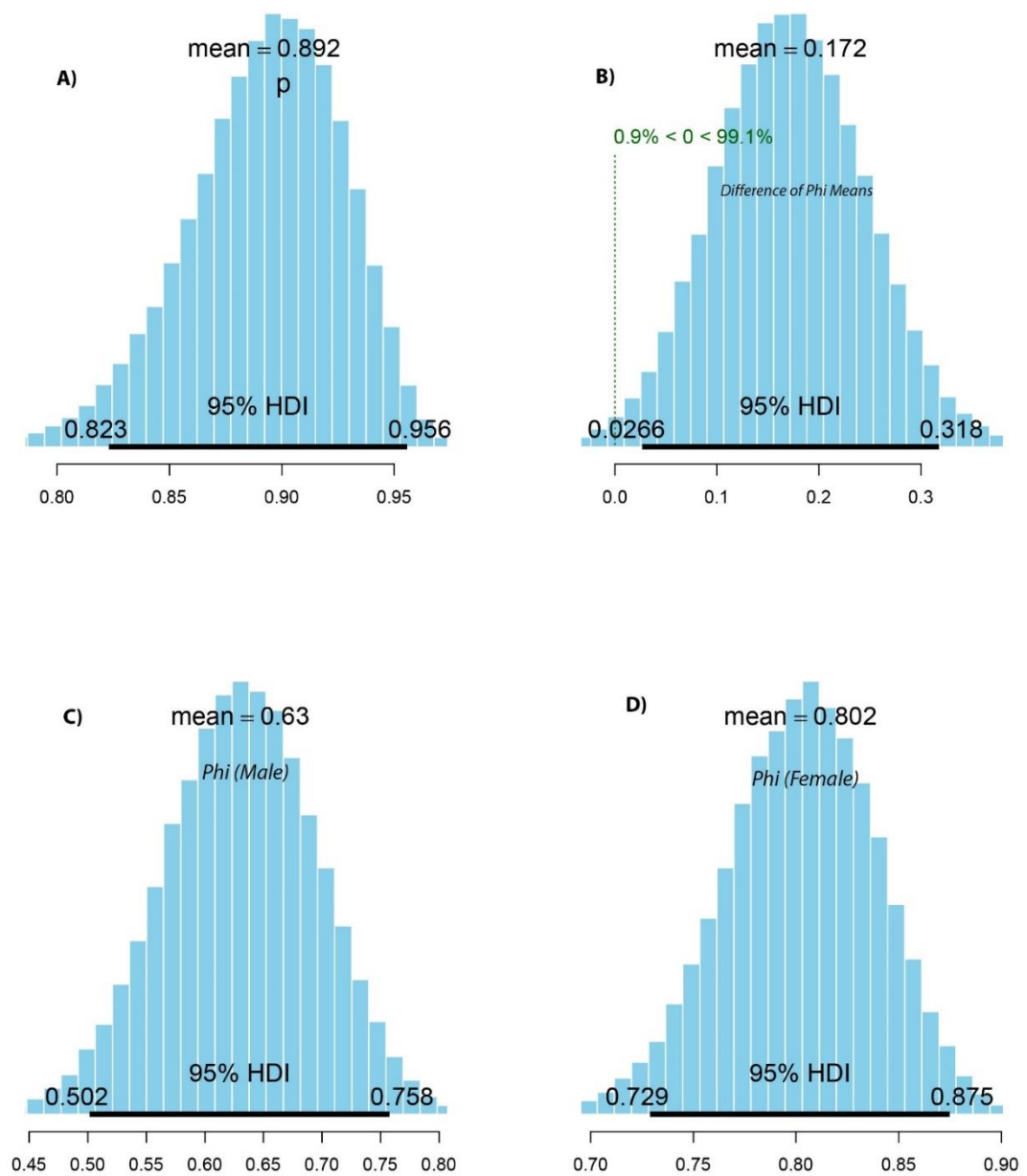


Figure 4.1. ROPE plot: sex-specific difference (leopards) in the posteriors of the survival parameters falling inside the region of practical equivalence (here the width of ROPE -1 to 1). (A) & (B) for fixed AC model (C) & (D) for Markovian AC model

Sex-specific recruitment of leopards (> 1year old) in Similipal Tiger Reserve

The mean annual recruitment was 12.26 (\pm 0.63 SE) individuals [26.64% (\pm 0.55 SE)] and 7.62 (\pm 0.86 SE) individuals [41.17% (\pm 2.88 SE)] for female and male leopards, respectively. Male leopards had a higher mean annual recruitment rate than females.

Table 4.5. Basic model (null) estimates of female leopard population \hat{N}_F , female leopard detection probability p_F , male leopard population \hat{N}_M , male leopard detection probability p_M obtained using Huggins closed-capture model from 2019-2022 along with the mean individual female/male leopard recruited annually in Similipal Tiger Reserve.

Year	M_{t+1} (F)	\hat{N}_F (SE)	p_F (SE)	M_{t+1} (M)	\hat{N}_M (SE)	p_M (SE)
2019	34	38.33 (2.62)	0.083 (0.010)	16	16.16 (0.41)	0.168 (0.019)
2020	34	41.74 (3.97)	0.065 (0.009)	16	16.18 (0.45)	0.163 (0.018)
2021	41	46.32 (2.91)	0.082 (0.009)	19	19.14 (0.38)	0.177 (0.017)
2022	48	50.11 (1.61)	0.118 (0.009)	20	20 (0.07)	0.277 (0.02)
Mean individual females recruited annually (SE)		12.26 (0.63)		Mean individual males recruited annually (SE)		7.62 (0.86)

Breeding female percentage of leopards in Similipal Tiger Reserve

I detected six lactating female/ female capture with cubs (< 1 year) for the initial three years. In 2022, eight lactating female/ females captured with cubs were detected in camera traps. The detection corrected mean annual breeding female percentage of leopards in Similipal Tiger Reserve was estimated at 61.43% (\pm 2 SE). Thus, the mean annual breeding female number corresponds to 27 (\pm 1.38 SE).

Discussion

Density estimation, population trend and sex-ratio of leopard in Similipal Tiger Reserve

Leopards were distributed throughout the study area. The sustained leopard presence in northern Similipal might be attributed to its more catholic diet (Hayward *et al.*, 2006) (see Chapter 5) along with their adaptability and behavioral plasticity (Athreya *et al.*, 2013; Athreya *et al.*, 2014). The leopard density in STR has not changed significantly from 2019-2022 and a stable population trend was observed during this period. The leopard density in Similipal (i.e., $5.12 \pm 0.59/100 \text{ km}^2$) is moderate on the country scale. However, relative to the estimates in the East-central landscape, the densities are on the higher side (Qureshi *et al.*, 2024). The detection corrected sex ratio of leopards remained female-biased, which is generally the case in the majority of studies on leopard populations across the globe (Schaller, 1972; Bailey, 1993; Anile & Devillard, 2018; Qureshi *et al.*, 2024).

Sex-specific apparent survival of leopard in Similipal Tiger Reserve

In extensive protected areas like Similipal, which also has marginal dispersal opportunities to habitats of similar quality, apparent survival is likely to closely reflect true survival rates (Schaub & Royle, 2014). The gender-specific survival revealed that male leopards had significantly lower annual survival probability, i.e., $0.630 (\pm 0.06 \text{ SD})$, than female leopards, i.e., $0.802 (\pm 0.03 \text{ SD})$. Usually, male leopards have a propensity to disperse further distance and possess larger home ranges than females (Table 4.1 for σ values), which translates to a heightened exposure to anthropogenic

threats, resulting in higher mortality (Balme *et al.*, 2010; Rostro-Garcia, 2021). Whereas, the females exhibit philopatry, typically remaining closer to their natal areas and holding smaller home ranges relative to male leopards (Fattebert *et al.*, 2015; Balme *et al.*, 2017a). In the Indian subcontinent, the sex-specific survival and recruitment rates of leopards are only available from the Kanha Tiger Reserve (Kumar, 2019) where a higher male leopard survivorship than females was observed. The estimates of male survivorship in the current study are lower than those reported by Kumar (2019), i.e., 0.70 (\pm 0.04 SE). However, the apparent survival of female leopards is significantly higher in Similipal than in Kanha i.e., 0.72 (\pm 0.05 SE). Studies worldwide have documented annual survival rates of leopards varying between 0.58 (\pm 0.07 SD) (Rostro-Garcia *et al.*, 2023) and 0.94 (\pm 0.04 SE) (Swanepoel *et al.*, 2013). The observed sex-specific apparent survival of leopards in this study falls within this limit. In the wild, apart from the risks involved in dispersal ventures, the other major reasons in a protected area for adult mortality include starvation (for older individuals), infighting, poaching, disease, and inter-specific strife with other large carnivores (Bailey, 1993; Swanepoel *et al.*, 2014). However, the exact reasons and their respective contribution to adult mortality are currently not known from Similipal.

Sex-specific recruitment of leopards in Similipal Tiger Reserve

The male leopards recorded higher sex-specific recruitment but lower apparent survival than female leopards and vice versa. The population trend remained stable over the sampling duration, indicating that the recruitments were most likely compensated for the losses of individuals in the population. The prey base in Similipal

has remained stable (see Chapter 2), and generally, in such regions with stable prey base, the leopard population also remains stable, with the recruitment matching the mortality. In Kruger National Park, the leopard population remained self-regulated due to adequate prey availability and maintained breeding adult population. The loss of females being balanced by young females produced in the region and the loss of young male leopards is corrected by the addition of males from the neighbouring area (Hornocker & Bailey, 1986; Bothma & Walker, 1999). I assume that similar dynamics might be governing the processes in the Similipal Tiger Reserve and the individuals from the buffer region of STR could be occupying the territories in the core region.

Breeding female percentage of leopards in Similipal Tiger Reserve

STR recorded a figure of 61.43% (± 2 SE) breeding female proportion in the population, which translates to ~27 females breeding every year in STR. Bailey (1993) reported a lower proportion of breeding females (~ 27.7%) in Kruger National Park. However, a higher breeding female percentage (~ 50%) (Friedmann & Traylor-Holzer, 2008) and even a rate of 100% ($n = 7$ females) producing cubs has also been observed (Owen *et al.*, 2010). The litter size of leopards ranges from 1-3 in most of the wild conditions (Bothma & Walker, 1999; Sunquist & Sunquist, 2002). Despite a high proportion of females in Similipal annually breeding, the population has remained stable. This might be attributed to a low survivorship of territory-holding adult males. This study shows that the male apparent survival is relatively lower than females, i.e., 0.630 (± 0.06 SE), indicating ~ 37% annual removal of males from the population annually. The leopards have a polygynous mating system with a single

male encompassing home ranges of multiple residential females and sire their cubs (Bailey, 1993; Sunquist & Sunquist, 2002). The stable male territories are vital for creating ideal conditions for the female to raise her cubs (Seidensticker & Lumpkin, 2004; Sunquist & Sunquist, 2014). Male leopards play a crucial role in provisioning females an environment free from intruding males, as they may threaten cub survival (Balme *et al.*, 2009). Infanticide in leopards is among the highest recorded for mammalian carnivores and has been reported to be the cause of death for thirty-three percent of leopard offspring in Sabi Sand Game Reserve (Balme & Hunter, 2013). The leopard cubs have been observed to be associated with the mother till the age of nineteen months. However, it has been found that cubs are prone to infanticide until they are 15 months old (Balme *et al.*, 2013). Thus, the prolonged presence/ survival of a territorial male would be crucial to increase the survival probability of its cubs.

The leopard populations are generally resilient to even higher mortality rates due to their relatively faster life-history parameters (i.e., short birth intervals and early age of reproduction, etc.) when compared to the larger big cats like the tiger. The advanced calculations have revealed that leopards could sustain an offtake of 22% of breeding females annually (Chapron *et al.*, 2008). The apparent survival of female leopards in Similipal is ~80% and only twenty percent of the females either die or emigrate. Thus, the current loss of female leopards (~ 20%) reported in this study lies above the mark below which the leopard population may decline. The number of annually breeding females in Similipal stands at ~27 individuals, and thus, Similipal supports a viable population of leopards. However, increased efforts in anti-poaching activities for protecting the prey and leopards would be pivotal to conserve this globally threatened large felid in Similipal Tiger Reserve.



Chapter- 5

Coexistence and Resource Partitioning Between Tiger and Leopard

Introduction

Intra-guild competition is one of the major ecological processes governing the structure and function of a community (Grassel *et al.*, 2015). Competition can lead to changes in species densities, distributions, behaviour, and population dynamics (Creel & Creel, 1996; Berger & Gese, 2007; Chesson & Kuang, 2008) and could be detrimental for one or both the species involved (Lovari *et al.*, 2015). Sympatric carnivores coexist by segregating resources at the spatial, temporal, and dietary axis (Durant, 1998; Vanak *et al.*, 2013; Periquet, 2015). In India, the tiger and leopard are sympatric in several parts of their distribution range (Ramesh *et al.*, 2012). The tiger, due to its physical superiority, is dominant over the leopard (Seidensticker, 1976), and it is usually observed that in areas where tigers are abundant, leopards occur in low densities and are displaced to edge habitats (Schaller, 1967; Johnsingh *et al.*, 2004).

Resource partitioning through dietary, temporal, and spatial segregation allows smaller species to co-exist and reduces the probability of lethal encounters with dominant species (Palomares & Caro, 1999). Significant dietary overlap exists between these sympatric large felids despite their varying body sizes (Karanth & Sunquist, 1995; Edgaonkar, 2008; Ramesh *et al.* 2009; Harihar *et al.*, 2011; Selvan *et al.*, 2013; Majumder *et al.*, 2013). However, variable patterns of prey selection tactics,

along with the availability of ample prey of different size classes, facilitate the co-existence of leopards and tigers in the same landscape (Karanth & Sunquist, 1995; Andheria *et al.*, 2007).

The leopard may also avoid tigers by using a different temporal scale (Vinitpornsawan & Fuller, 2020). However, in the Mae Wong and Khlong Lan National Parks, no active temporal segregation between the tiger and the leopard was recorded (Phumanee *et al.*, 2021). Leopards are also reported to avoid areas with high tiger abundance and are pushed into suboptimal habitats (Seidensticker, 1976; Harihar *et al.*, 2011). However, competition for space could be more intense in suboptimal areas (Ramesh *et al.*, 2012). After tiger reintroduction in Sariska, leopard abundance drastically declined, and areas dominated by tigers were selectively avoided (Mondal *et al.*, 2012).

Habitat heterogeneity also reduces the chances of interaction between the tiger and leopard and decreases the dominance effect of tigers (Seidensticker, 1976). Sunquist and Sunquist, (2002) concluded that the leopard co-exists with the tiger by avoiding their hunting and resting areas. Moreover, fine-scale behavioral segregation is also used by these sympatric large felids to co-exist (Karanth *et al.*, 2017). It has been suggested that in areas of low prey density, intra-guild competition may intensify (Vanak *et al.*, 2013; Karanth *et al.*, 2017). In the current scenario, the surging human population and consequentially rising anthropogenic disturbances have greatly increased habitat fragmentation. It has led to the creation of isolated habitats which are smaller than naturally functioning ecosystems (Hayward & Slotow, 2009). Thus, this coercive shoving of top predators in much smaller areas increases the intensity of

hostile interactions among them, which may stimulate the extinction process (Creel, 2001; Caro & Stoner, 2003). Active management is required for these naturally deficient ecosystems (Walters, 1986). Thus, it would be crucial to understand the drivers of co-existence between tiger and leopard in the Similipal Tiger Reserve.

Methods

Assessing spatial separation between the tiger and leopard in Similipal Tiger Reserve

Spatially explicit capture re-capture density (Borchers & Efford, 2008) for details (refer to Chapters 3 & 4) were obtained using the data for the year 2021. The 2021 data was selected as the tiger population was highest during this sampling year in southern STR. I obtained pixel-wise density at the scale of spacing (500*500m) used for running the analysis. The pixel density is for every point in the state space model for both the tiger and leopard. The pixel density is obtained using *fx.total* function within the package *secr* version 4.3.3 (Efford, 2024) in R to generate a spatial realization of the overall density surface. This surface encompasses the minimum bounding polygon that defines the camera trap locations, expanded by a one-kilometre buffer zone. I opted not to generate a density surface for the entire model-fitted mask area because information on animal distribution outside of camera trap zone was unavailable. The selection of one-kilometre buffer around the minimum trapping area was justified based on the analysis of home range center probability contours for detected animals, along with an equivalent scaled probability for undetected individuals. I plotted the generated tiger density at x-axis and leopard density at y-axis in the scatter plot. The scatter plot is the best way to explore the relationship

correlation of dependent variable (here leopard density) on the independent variable (here tiger density).

Assessing temporal overlap between tiger and leopard in Similipal Tiger Reserve

The photographs obtained from the camera traps have the time of capture stamped on them. This information was used to assess the temporal activity pattern of tigers and leopards in Similipal Tiger Reserve. The photo-capture of the same individual tiger/leopard was identified as an independent event only when it was captured after an interval of 30 minutes from the previous event (O'Brien, 2003). The analysis of activity patterns was done using the package “overlap” (Meredith *et al.*, 2024) in R (R Core Team 2023). As suggested by Meredith & Ridout (2020), I used the Dhat 4 estimator due to the number of detections being >75 for all the combinations. The package overlap offers functionalities to fit kernel density functions on the temporal activity pattern data and, estimates overlapping density coefficients between two species, and generates bootstrap confidence intervals. The CI 95% for every overlap estimate was done using 10,000 bootstrap iterations.

Assessing the principal prey and most utilized prey of tiger and leopard in Similipal Tiger Reserve

Kill identification, field observation, stomach content analysis, and scat analysis are some common methods used to understand the diet of large carnivores. By virtue of being cost- and time-efficient, scat analysis is considered to be among the most robust methods for dietary studies (Schaller, 1967; Kruuk, 1972; Sunquist, 1981; Johnsingh, 1983, 1992; Karanth & Sunquist, 1995). The hair of the prey species remains

undigested even after passing through the gut of the carnivore and is among the best entities to identify the consumed species (Ramakrishnan *et al.*, 1999). Thus, the food habits of large felids of STR were assessed by analysing field-collected scats.

Collection of predator fecal samples

Scats were collected during large carnivore sign surveys conducted between 2019 and 2022. Surveys involved walking along animal trails, forest roads, and fire-lines, which are typically used by large carnivores to move through the landscape (Johnsingh, 1983). Details such as Date, Range, GPS location, place where found, condition of scat (fresh or old), associated carnivore sign, and substrate type were also recorded. All the faecal samples were collected in wax-paper sheets and sterile zip-lock bags before keeping them in dry boxes for further dispatch to the laboratory, where they were stored at -20°C freezer (Biswas *et al.*, 2019).

Species confirmation

The scats were genetically ascertained using tiger- and leopard-specific mitochondrial molecular markers to ensure the usage of species-specific samples to assess their respective dietary patterns. I used a modified Qiagen DNA extraction protocol to extract DNA from the scat samples (Biswas *et al.*, 2019). Two mitochondrial tiger-specific primers of the NADH5 region of 225 bp (Tig490F/R) and 164 bp (Tig509F/R) (Mukherjee *et.al.*, 2007) and one mitochondrial primer of the NADH4 region of 85 bp (TigND4) (Mondol *et al.*, 2014) were used to precisely identify tiger scats. I also used a mitochondrial primer of the NDH4 (ParND4) region of 130 bp (Mondol *et al.*, 2014) for determining leopard scats.

Prey identification

Subsequently, all the leopard- and tiger-positive fecal samples were oven dried for 72 hours at 60°C. I implemented a modified frequency of occurrence measure known as percentage whole scat equivalence to estimate the contribution of each species in the respective large felid diet, thereby considering the relative amount of each prey category in the scat without any overestimation (Angerbjorn, 1999). I did this by opening the scat and analyzing different parts that differed in composition. The prey species were identified by hair medullary pattern, cortex pigmentation, hair color, and relative hair size (Mukherjee *et al.*, 1994). The hair character, like medullary structure (Mukherjee *et al.*, 1994) was the major feature through which microscopic examination of prey hair was performed as it proved to be the best feature to ascertain the prey species without ambiguity in study areas with similar prey community as found in STR (see Biswas *et al.*, 2023). To ensure the optimal collection of hairs from scat, at least 20 hairs were picked up in above mentioned manner for the slide preparation (Jethva & Jhala, 2003). Before placing the hairs on slides, the dirt on the hairs was cleaned with water and then hair was immersed in alcohol to dehydrate. Furthermore, the hairs were cut at both ends and washed with xylene so that xylene enters the hair and makes the medullary pattern clearly visible through the microscope.

I used the reference manual developed by (Bahuguna *et al.*, 2010) to correctly identify consumed species from hair characteristics. I also prepared reference slides for all potential prey species in STR from hair samples obtained from dead prey species recorded in the field as well as from the repository of Research laboratory of Wildlife

Institute of India. Sample size sufficiency was estimated for diet analyses by using a sample rarefaction curve (Hurlbert, 1971; Heck Jr *et al.*, 1975) in R (version 4.0.2) using the “*vegan*” package (Oksanen *et al.*, 2013).

Principal prey and most utilized prey of large felids in Similipal Tiger Reserve

I used $\frac{3}{4}$ of the mean weight of female prey from the literature, i.e., Schaller (1967) and Awasthi *et al.* (2016), as biomass of prey. I estimated biomass consumption from scats for tigers and leopards using the generalized model and the leopard-specific model developed by Chakrabarti *et al.* (2016). The generalized equation used for the tiger could be written as $y = 0.033 - 0.025 * \text{EXP}(-4.284 * x / \text{PBW})$, where y = prey biomass consumed per collectable scat, x = prey biomass and PBW = predator biomass. The leopard-specific model is calculated from the equation $y = 2.171 - 1.671 * \text{EXP}(-0.056 * \text{prey biomass})$, where y = prey biomass consumed per collectable scat. I implemented Ivlev's selectivity index (Ivlev, 1961) for assessing most utilized prey of the large felids. The formula for calculating Ivlev's selectivity index (PI) is $PI = \frac{U - A}{U + A}$, where U = utilized biomass of prey, A = available biomass of prey. I used the principal prey estimates for the entire tiger reserve (Table 2.7) to calculate the available biomass. Since the tigers were not found in the northern part of Similipal from 2019-2021, I also did a catchment-wise (northern and southern) principal prey estimation for leopard. It enabled me to understand the diet of leopard in presence and absence of tiger in the same protected area i.e. Similipal Tiger Reserve.

Dietary overlap among large felids

I used the package “*pgirmess*” (Giraudoux, 2024) in R programming environment and estimated Pianka’s index (Pianka, 1973) to assess dietary overlap. The Pianka index ranges from 0 (no overlap) to 1 (complete overlap).

Results

Assessing spatial separation between the tiger and leopard in Similipal Tiger Reserve

After examining the scatter plot (Figure 5.1) it is evident that high densities of leopards occurred at very low densities of tigers (exponential decay of leopard density toward high tiger density). However, there are some places where both leopard and tiger occurred at very low densities, which may be due to low prey availability, human disturbance and, hostile terrain etc. Thus, the leopard density declines spatially with increasing tiger densities, which indicates avoidance of the regions by leopards with increasing densities of tigers in Similipal and, thereby facilitating coexistence.

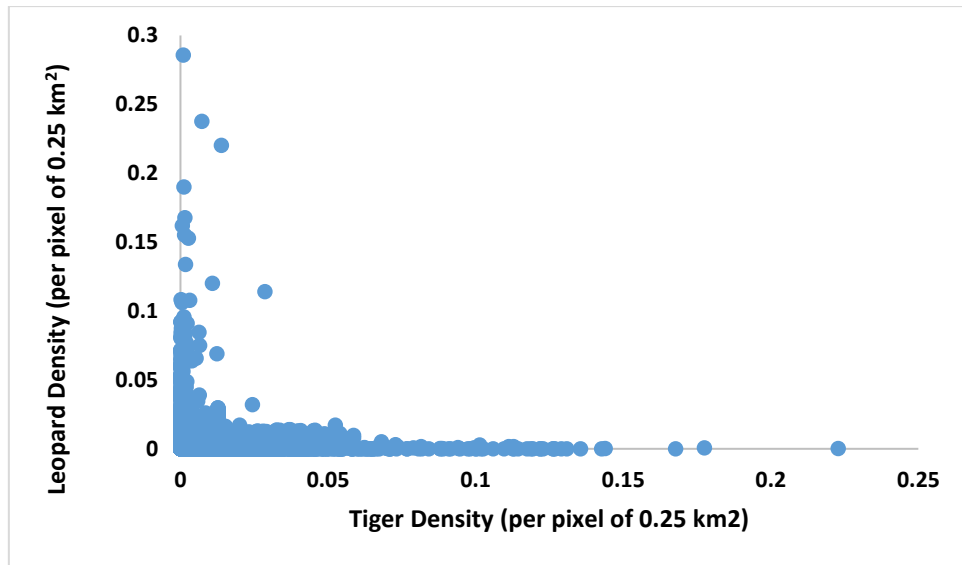


Figure 5.1. Scatter plot of tiger density versus leopard density generated at 500 m 500 m grid in southern core (tiger occupying area) of Similipal Tiger Reserve.*

Assessing temporal overlap between tiger and leopard in Similipal Tiger Reserve

The leopard and tiger showed a high degree of temporal overlap in Similipal of 88% i.e., $D_{hat\ 4} = 0.88$ ($CI_{95\%}$ range (0.84- 0.96)) (Figure 5.2). The tigers were observed to have a bimodal peak in activity pattern i.e., starting during the dawn and reaching a major peak between (18:30- 20:00). The other minor peak was reached after initiating at midnight, reaching the maximum value between (2.00- 3.00). The tigers rested throughout the late morning and afternoon hours, and in general, exhibited a nocturnal activity pattern in Similipal. The leopards showed a bimodal peak in activity. The major peak initiated between 14:00 and reached its maximum during the late evening (18:00- 19:00). A second minor peak reached the maximum value between (3:00- 5:00) in the night. Overall, a greater part of the leopards were nocturnal but exhibited more diurnal activity when compared to the tiger.

However, a separate analysis for assessing the degree of overlap of leopard with tiger based on gender (male leopard and female leopard) was also conducted. I found that the male leopard had a very high overlap of 93% i.e., $D_{hat} 4 = 0.93$ (CI95% range (0.90- 1.0)) and is very similar to the activity pattern of the tiger (Figure 5.3). However, the temporal overlap of female leopard with tiger was estimated at 77% i.e., $D_{hat} 4 = 0.77$ (CI95% range (0.67- 0.88)) and is significantly lower than that of male leopard (Figure 5.4). The female leopards are more diurnal relative to the male leopards.

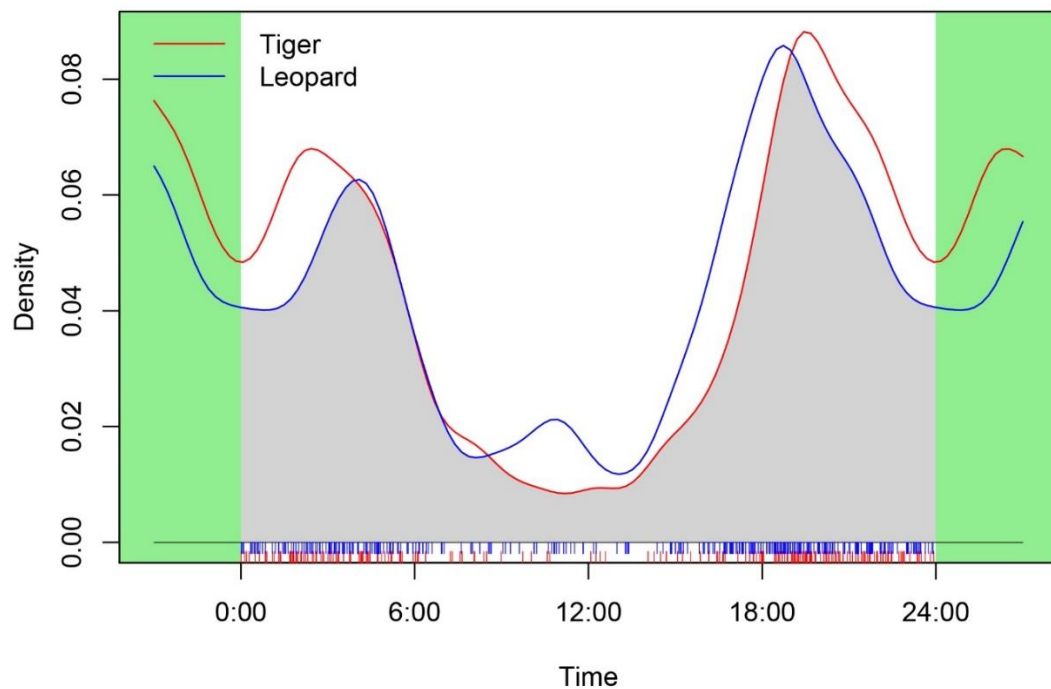


Figure 5.2. Activity overlap of tiger and leopard in 24hrs day cycle in Similipal Tiger reserve

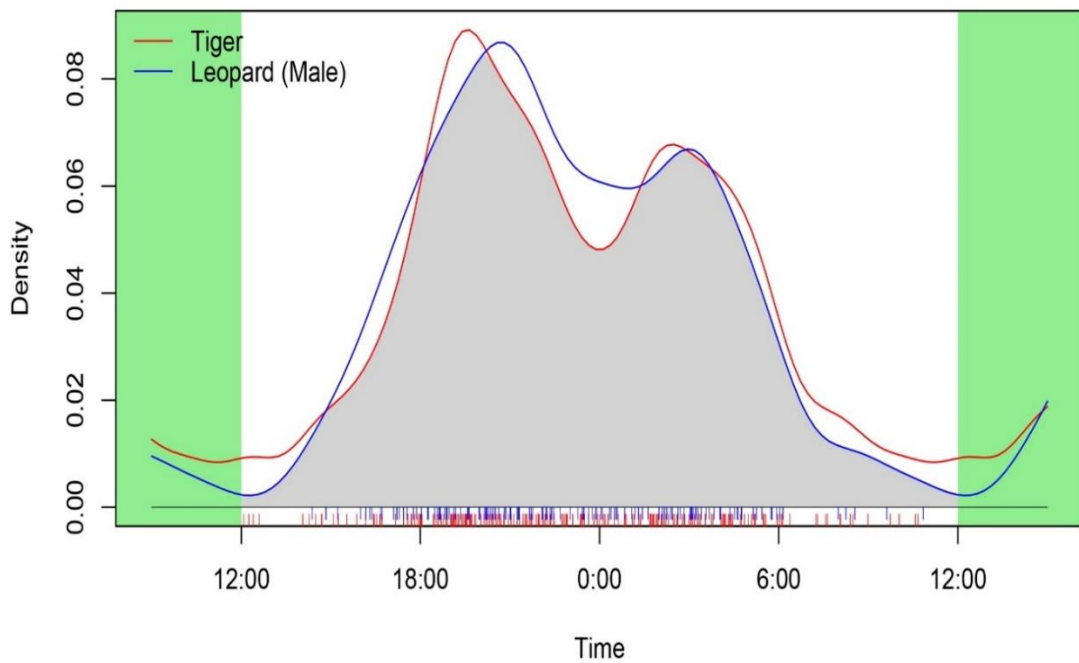


Figure 5.3. Activity overlap of tiger and male leopards in 24hrs day cycle in Similipal Tiger reserve

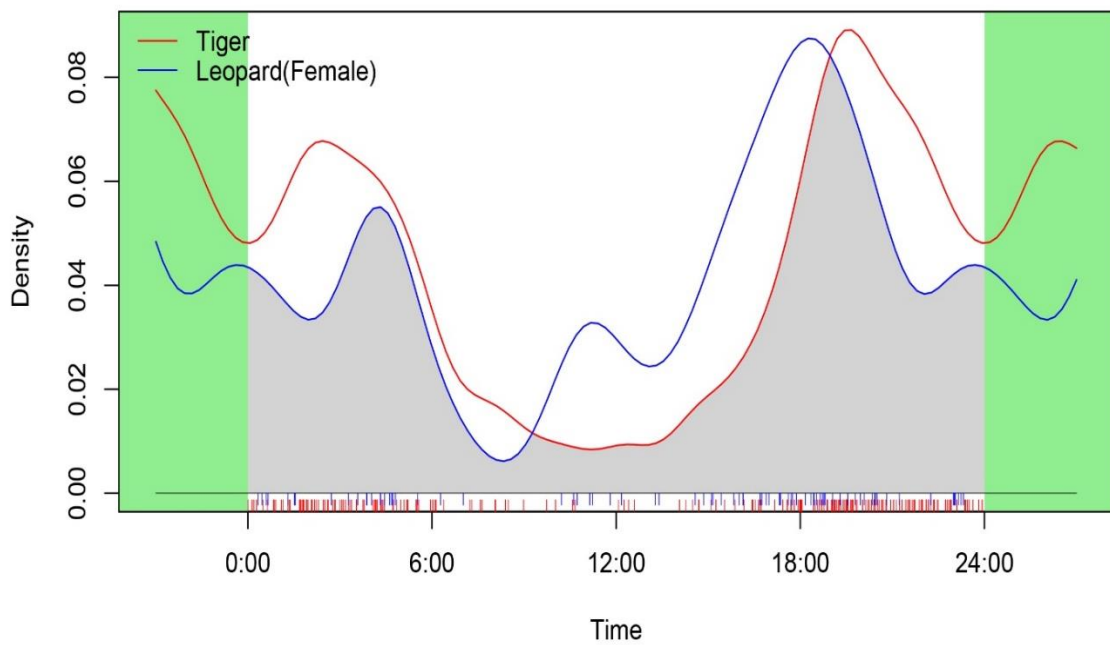


Figure 5.4. Activity overlap of tiger and female leopard in 24hrs day cycle in Similipal Tiger reserve

Assessing the principal prey and most utilized prey of tiger and leopard in Similipal Tiger Reserve

I collected 400 large carnivore scats to analyze the prey remains. Of these, 61 were genetically assigned to be of the tiger, and 194 were identified to be of leopard. Because I could not identify the exact prey species for four tiger and six leopard scats, the dietary analysis was based on 57 tiger scats and 189 leopard scats. The principal prey is the one which relatively contributes most to a predator's diet. The prey species were divided into the three categories mentioned below based on their body weight following (Lovari *et al.*, 2015).

- Large Prey- (weighing >100 kg)
- Medium sized prey- (weighing >25 kg and = 100 kg)
- Small Sized Prey- (weighing < 25 kg)

Five ungulate species (i.e., chital, sambar, northern red muntjac, wild pig, and gaur) were consumed by the tigers in STR. Sambar is the principal prey of the tiger and constitutes 55.02% of its diet. Chital, in second place, formed 17.91% of the tiger's diet. On the whole, large-bodied prey formed ~ 67% of the tiger's diet, whereas the medium-sized prey contributed 25.60% to the diet. Small-sized prey forms only ~ 7% of the tiger diet (see Figure 5.9.). Livestock was not recorded in the tiger diet as the tiger was recorded in the northern core (considerable livestock movement region) only in the last sampling year. However, the contribution of livestock in its diet may increase in the future due to the re-occupancy of northern Similipal by tigers. For the tiger diet, the maximum contribution was of sambar followed by chital > gaur > wild

pig > northern red muntjac. Sambar and northern red muntjac were positively utilized by the tiger, whereas the chital and wild pig were negatively used (Figure 5.11).

Leopards were recorded to feed on twelve different prey species in entire STR. I estimated the principal prey of leopards in the the entire STR and in the northern and southern catchments separately. In total, 194 scats were determined to be of leopards, out of which the prey item was identifiable in 189 scats. The exact location of thirteen leopard scats was unknown, and thus, they were discarded for catchment-wise analysis.

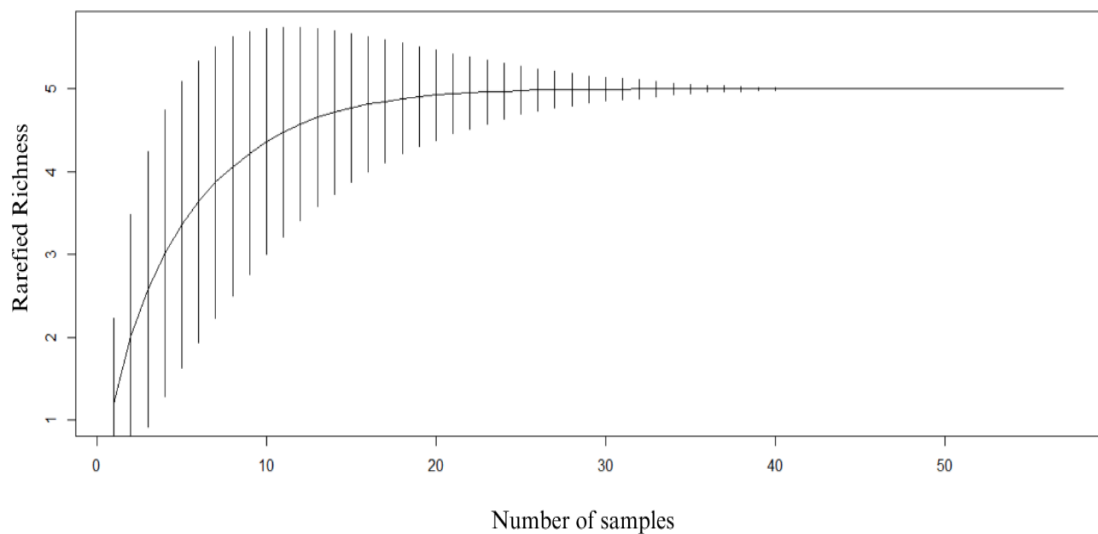


Figure 5.5. Rarefaction curve depicting prey species richness found in the scats of the tiger in Similipal Tiger reserve, Odisha, India (based on 10000 iterations).

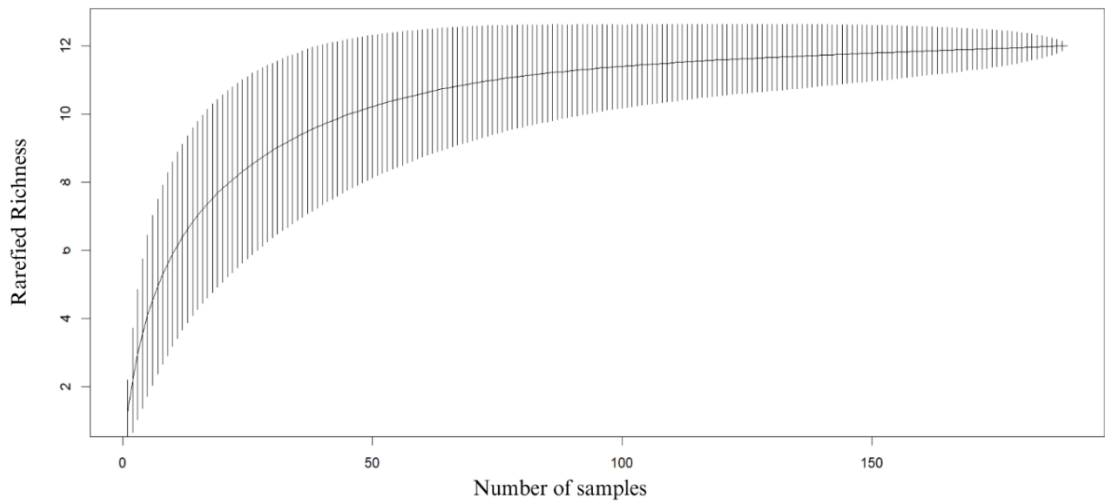


Figure 5.6. Rarefaction curve depicting prey species richness found in the scats of leopard in Similipal Tiger reserve, Odisha, India (based on 10000 iterations).

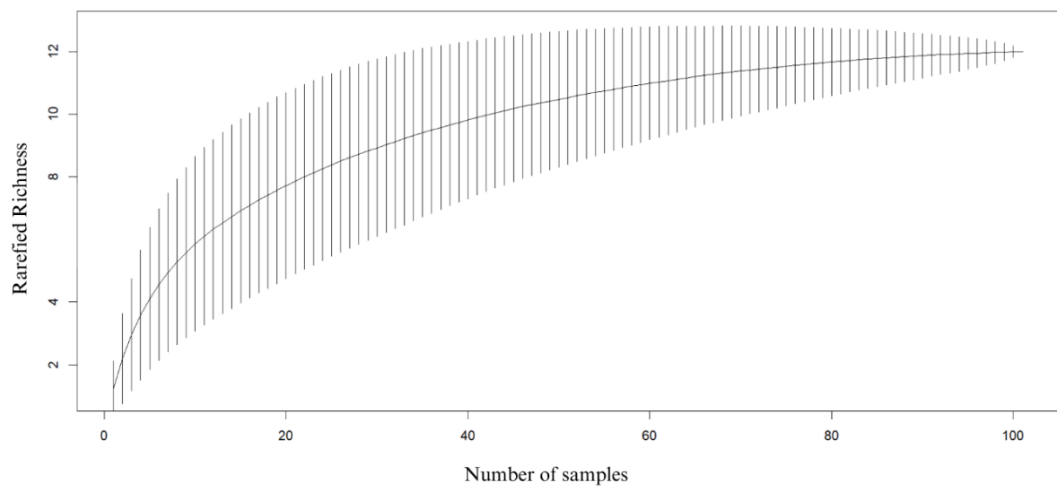


Figure 5.7. Rarefaction curve for prey species richness found in the scats of the leopard in southern part of Similipal Tiger reserve, Odisha, India (based on 10000 iterations).

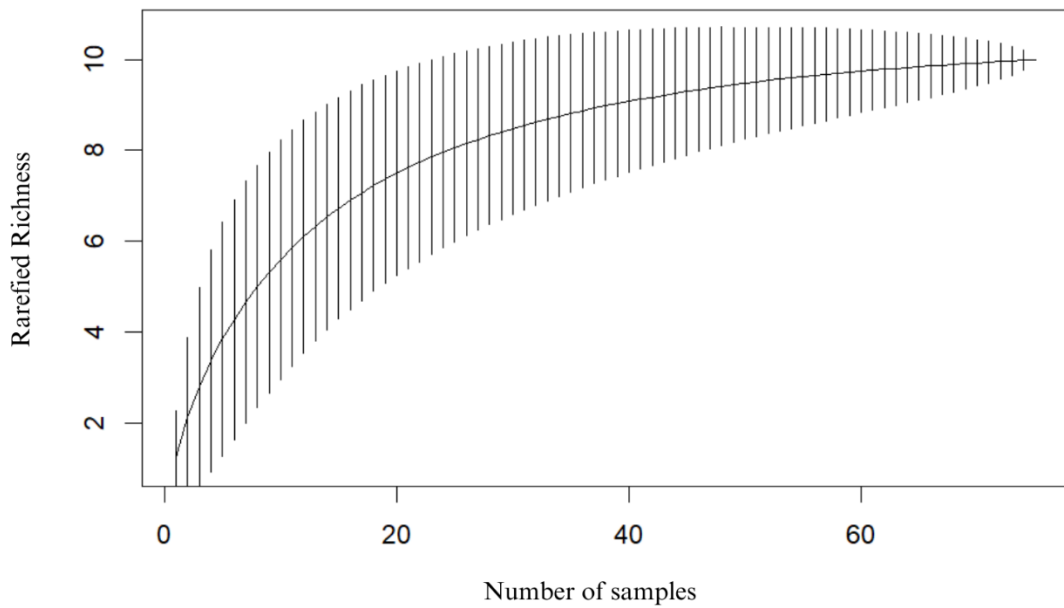


Figure 5.8. Rarefaction curve for prey species richness found in the scats of leopard in northern part of Similipal Tiger reserve, Odisha, India (based on 10000 iterations).

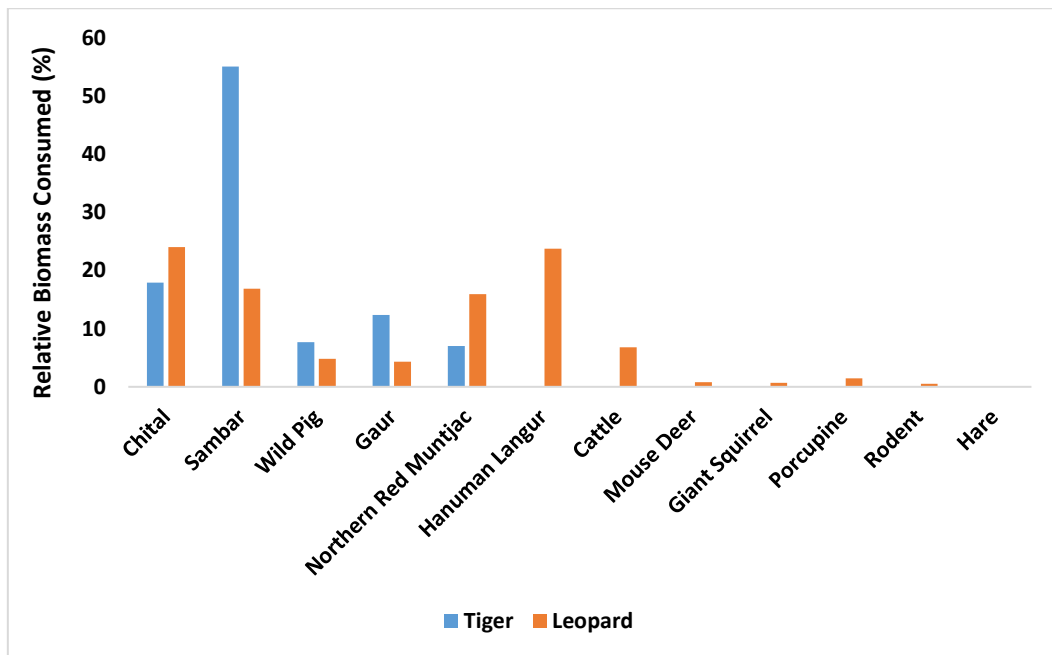


Figure 5.9. Relative biomass consumed (%) of different prey by tiger and leopard in entire STR.

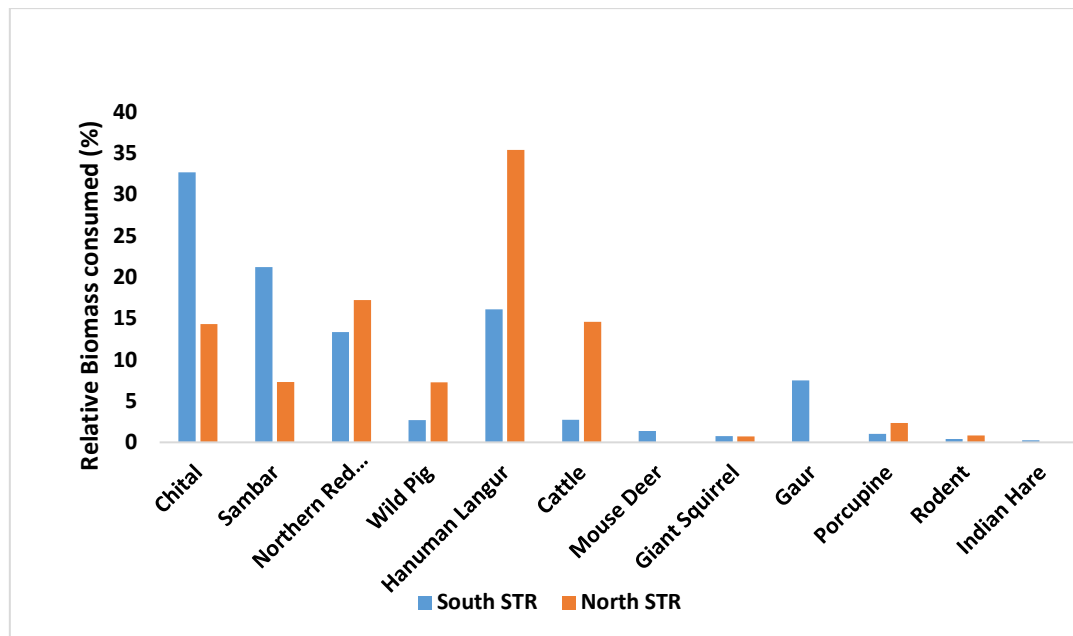


Figure 5.10. Relative biomass consumed (%) of different prey species by leopard in

Southern STR and Northern STR

I obtained 75 and 101 leopard scats from the northern and southern catchment, respectively. In the entire STR, the maximum contribution to the leopard diet was of chital (23.99%) and langur (23.71%), followed by > sambar > northern red muntjac > cattle > wild pig > gaur. Other small prey formed only 3.63 % of the leopard's diet in the entire STR (Figure 5.9). However, in the northern catchment, the langur formed 35.38% of the leopard diet. This was further followed by northern red muntjac > cattle > sambar = wild pig (Figure 5.10). Other small prey formed only 3.96% of leopard's diet in the northern catchment. In the southern STR, chital was the principal prey in the leopard diet, contributing 32.66%, followed by sambar > langur > northern red muntjac > gaur > wild pig > cattle (Figure 5.10). Other small prey formed only 3.76% of leopard's diet in the southern catchment. In the entire STR, the Hanuman

langur, northern red muntjac, and chital were positively utilized by the leopard, and the wild pig and sambar were negatively used (Figure 5.11).

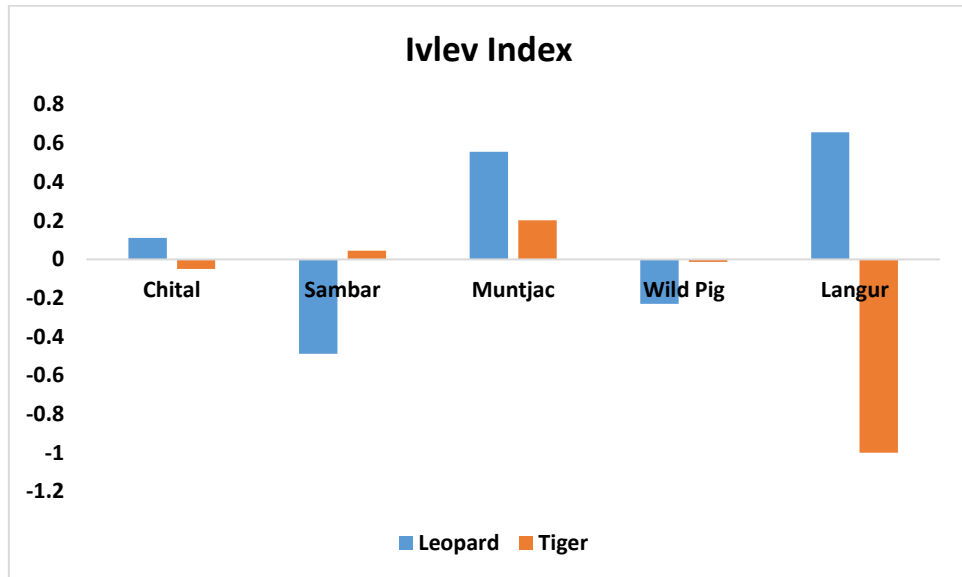


Figure 5.11. Ivlev's index for prey utilization by leopard and tiger in Similipal Tiger Reserve.

Dietary overlap among large felids

The dietary niche overlap between the tiger and leopard, as estimated by Pianka's niche overlap, was moderate with a value of 0.602 (i.e. 60%).

Discussion

The study helps to understand the mechanism of resource partitioning among the large felids. A comparison of the leopard and tiger spatially explicit densities extracted at a fine scale (500 m* 500 m grid) revealed the avoidance of leopards to the high tiger density regions. Similarly, Kumar *et al.* (2019) observed that leopards reached their highest densities in regions where the tiger densities were low/ declining, and the population growth rate of leopards were highest recorded in areas with stable/ low/ declining tiger densities. My results corroborate with the findings of earlier studies reporting the avoidance of high-density tiger areas by leopards (Schaller, 1967; Seidensticker, 1976). However, Similipal is a low tiger density region and there is high variability in the distribution of tiger densities in space. Thus, the leopard could coexist with the tiger in the same landscape, which is further facilitated by its adaptable nature and dietary plasticity.

The temporal activity pattern between the tiger and leopard revealed a high degree of overlap i.e., ~ 88%. However, it was observed that the male leopards have a significantly greater temporal overlap with the tiger (~93%) when compared to the female leopards (~77%). The female leopards were relatively more diurnal than the tigers and male leopards, as observed in some other studies (Havmøller *et al.*, 2020; Rouse *et al.*, 2021). Female leopards usually have smaller home ranges compared to males and generally invest a lot of time and energy to raise cubs (Bailey, 1993; Oftedal & Gittleman, 1989; Balme *et al.*, 2017a). Thus, their temporal activity pattern would have definite fitness consequences when compared to males and would significantly affect the recruitment processes in the population.

The larger predators, such as, lions have been known to account for 22% of known leopard cub mortality as well as 23% of leopard (≥ 2 years old) deaths (Balme *et al.*, 2017b). Moreover, the infanticide by male leopards is among the highest recorded among mammalian carnivores (Balme & Hunter, 2013). Predation-mediated leopard cub mortalities have been estimated to reach as high as 91% of the total deaths (Balme *et al.*, 2013). The tiger, being the larger predator, could pose a similar threat to female leopards and their cubs. The females may also avoid other male leopards spatially and temporally to reduce the probability of death from infanticide (Rouse *et al.*, 2021). Thus, female leopards may partition their temporal activity from that of larger predator and male leopards by having different peak activity periods. Since the temporal activity pattern of male leopards approximately mirrors that of the tiger, the female leopard utilizes different times of the day (mostly diurnal) and activity peak periods to possibly reduce the chances of lethal encounters.

The tigers in STR fed upon five ungulate species, i.e., chital, sambar, northern red muntjac, wild pig, and gaur. Sambar and chital combined formed greater than seventy percent of the tiger diet in Similipal. The leopard, on the other hand, preyed upon twelve different prey species, and the Hanuman langur turned out to be the principal prey, followed by chital. The dietary overlap between the two species was estimated at 0.602 (i.e. 60%), which is significantly lower than reported in earlier studies (Lovari *et al.*, 2015; Simcharoen *et al.*, 2018; Lamichanne *et al.*, 2019.). An earlier study in Similpal (Palei *et al.*, 2023) which used physical appearance of scats to assign them into appropriate species (i.e. tiger & leopard) recorded nearly similar value of dietary overlap (0.55; i.e. 55%). However, Palei *et al.* (2023) did the sample collection only from southern part of Similipal, and this study used samples

distributed across northern to southern regions of STR. Thus, on comparing the estimates of dietary overlap from the above-discussed study, the estimates from STR are on the lower side. However, this overlap has been estimated by using tiger scat samples (largely confined to southern Similipal during the study) and leopard scat samples from entire Similipal, including the tiger-devoid regions of northern STR.

Large ungulate prey in high densities is a prerequisite to harbor viable populations of large carnivores (Karanth & Stith, 1999; Karanth *et al.*, 2004). Sambar forms > 50% of the tiger's diet in Similipal. Almost 60% of studies on tiger diet identified sambar as the principal prey (Simcharoen *et al.*, 2014) and our study reiterates the same. Moreover, tigers have been known to prefer larger-bodied prey species which assists them to maximize gains for the energy expended (optimal foraging). Sambar has been identified as one of the most preferred prey of tigers. A viable sambar population through its distributional range would assist in sustaining tigers for the long-term in different landscapes (Hayward *et al.* 2006). No traces of Hanuman langur were found in any of the tiger's scat, indicating avoidance.

Chital contributed a significant 18% of the relative biomass consumed by the tiger but was marginally underutilized (Figure 5.11). These may be due to the similar individual densities of chital and sambar in STR. Further, sambar also had a significantly higher group density and encounter rate than chital (Table 2.7). Thus, the probability of a predator encountering a herd of sambar is more than that of chital and, which is probably getting reflected in the principal prey and most utilized prey of the tiger. Northern red muntjac which contributed very little (~ 7%) to the diet of tiger was positively utilized. The muntjacs are known to be utilised by tigers in proportion

to their availability (Hayward *et al.* 2012) and many studies have reported tigers to feed on muntjacs (McDougal & Seidensticker, 1975; Rabinowitz, 1989; Seidensticker & McDougal, 1993; Lovari *et al.*, 2015). Northern red muntjacs occur at high densities in Similipal relative to many other habitats in the country (Jhala *et al.*, 2020) and has the highest encounter rate among all the prey species found in STR (Table 2.7). Thus, they might have been utilized positively in the tiger's diet despite being present in only ~ 10% of the tiger's scats analyzed. Apart from northern red muntjac, other small prey were not encountered in the tiger's diet.

Twelve different prey species were recorded in the diet of leopards in the entire STR. Chital and Hanuman langur were found to be the principal prey and contributed almost equally to the relative biomass consumed by leopards. The larger-bodied prey such as the sambar, gaur, and cattle combined constituted ~ 28% of the leopard diet. Similarly, the medium-sized prey (chital and wild pig) also formed ~ 29% of the diet. Due to the high predation rate on langur, the smaller-bodied prey represented the greatest portion (~ 43%) of leopard's diet. Leopards have a wide dietary breadth and catholic diet (Hayward *et al.*, 2006). Moreover, their arboreal ability also allows them to predate upon primates (Schaller, 1967; Zuberbühler & Jenny, 2002; Puri *et al.*, 2020). Leopards were also recorded to feed on livestock (~ 7% biomass consumption) due to their distribution in the northern STR as well as the buffer zone which are frequented by cattle. The most utilized prey of leopards in the entire STR were northern red muntjac > hanuman langur > chital. Sambar and wild pig were utilized less in proportion to their availability. Leopards prefer a prey range weighing between 10- 40 kg, and our findings aligns with it (Hayward *et al.*, 2006).

The catchment-wise analysis of the leopard diet showed that the larger-bodied prey constituted ~ 31% and ~ 21% part of the relative biomass consumed by leopards in southern STR and northern STR, respectively. Moreover, the majority of large prey contribution in the diet of leopards in northern STR is not of wild prey but due to a higher proportion of livestock consumption (14.59%) when compared to southern STR (2.72%). Gaur contributed 7.50% of the relative biomass consumed in the leopard diet in southern STR. The leopards might be scavenging on the gaur kills made by the tiger and they are also known to predate upon gaur calves (Ahrestani & Karanth, 2014). Chital was the principal prey of leopards in southern STR, whereas the Hanuman langur was predated upon most in northern STR. Similarly, the contribution of sambar was also significantly reduced in northern STR compared to southern STR. Species like wild pig and northern red muntjac, which are resilient to anthropogenic influences, had significantly higher contributions in diet of leopards in northern STR than in southern STR.

The above discussed patterns could be attributed to the very low density of ungulate prey (particularly chital and sambar) in northern STR compared to southern STR (Figure 2.3). Due to the low abundance of medium-large ungulate prey in northern STR, leopards are mostly dependent on Hanuman langur (similar density in northern STR and southern STR; Figure 2.3) to fulfil their energetic requirements. Moreover, it has been reported that leopards are mostly dependent on primates in regions depleted with ungulate prey (Seidensticker, 1983; Hayward *et al.*, 2006). Currently, the cattle forms ~ 15% of the leopard's diet in northern STR, which is surrounded by villages (Figure 1), and the loss is compensated to the owner in monetary forms. The study highlights the importance of a high density of Hanuman langur in northern STR, as

their decline could potentially lead to the leopard switching their diet to cattle and intensify the human-wildlife conflict situations. This would also lead to greater monetary compensation being provided by the government to the concerned victims. Thus, the study highlights the importance of ungulate/ arboreal prey to keep the human-wildlife conflict at low levels (Puri *et al.*, 2020). The observed dietary differences observed in leopard's diet in northern STR and southern STR are a result differential prey availability rather than the effect of tigers.



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Journal of Threatened Taxa

10.11609/jott.2024.16.6.25283-25494
www.threatenedtaxa.org

26 June 2024 (Online & Print)
16(6): 25283-25494
ISSN 0974-7907 (Online)
ISSN 0974-7893 (Print)



Open Access



ISSN 0974-7907 (Online); ISSN 0974-7893 (Print)

Publisher
Wildlife Information Liaison Development Society
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Cover: Emperor Tamarin *Saguinus imperator*: a look into a better world through the mustache lens – mixed media illustration. © Maya Santhanakrishnan.



Empirical evidence of Tiger *Panthera tigris* (Mammalia: Carnivora: Felidae) dispersal towards south from Similipal Tiger Reserve to Kuldiha Wildlife Sanctuary: potential implications for its conservation in the Greater Similipal Landscape

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Abstract: India has achieved a rare global conservation success by doubling its Tiger *Panthera tigris* number since 2006. However, in India's east-central states of Odisha, Chhattisgarh, and Jharkhand the tiger numbers are declining. The tiger population in Odisha is largely confined to Similipal Tiger Reserve which represents the only known breeding population of a genetically unique wild melanistic form. We report a first empirically confirmed tiger dispersal event towards the south between Similipal Tiger Reserve and adjacent Kuldiha Wildlife Sanctuary as part of our intensive monitoring exercise conducted from 2019–2022. This evidence-based dispersal event confirms tiger presence in Kuldiha after 11 recent years and urges strong support for tiger conservation in the Greater Similipal Landscape. In order to ensure long-term tiger presence in this landscape, we suggest more rigorous management interventions like habitat restoration and management, prey recovery, intensive protection measures, conflict management, and creation of inviolate space.

Keywords: Eastern Ghats Landscape, east-central tiger population, functional corridor, habitat integrity, Hadgarh Wildlife Sanctuary, human-tiger conflict mitigation, melanistic tiger population, metapopulation dynamics, prey recovery, systematic camera-trapping

Editor: L.A.K. Singh, Bhubaneswar, Odisha, India.

Date of publication: 26 June 2024 (online & print)

Citation: Rathore, H.S., J. Pati, S. Gowda, D.N.S. Kiran, M. Yogajayananda, Y.V. Jhala, M.V. Nair, B. Pandav & S. Mondol (2024). Empirical evidence of Tiger *Panthera tigris* (Mammalia: Carnivora: Felidae) dispersal towards south from Similipal Tiger Reserve to Kuldiha Wildlife Sanctuary: potential implications for its conservation in the Greater Similipal Landscape. *Journal of Threatened Taxa* 16(6): 25299–25304. <https://doi.org/10.11609/jott.8949.16.6.25299-25304>

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Funding: Funding for this work has been provided by the National Tiger Conservation Authority, Government of India through the Odisha Forest Department.

Competing interests: The authors declare no competing interests.

Author details: See end of this article.

Author contributions: All enlisted authors have collaborated in developing and designing the paper. Data generation, data curation, formal analysis, validation, visualization, writing original draft, writing-review and editing [Harshvardhan Singh Rathore]. Data curation, writing - review and editing [Jagyandatt Pati, Samrat Gowda, Sai Kiran DN, M. Yogajayananda, Yadvendradev V. Jhala, Manoj Nair]. Conceptualization, writing-review and editing, supervision, funding acquisition [Bivash Pandav]. Conceptualization, resources, writing - original draft, writing -review and editing, supervision, project administration, funding acquisition [Samrat Mondol].

Acknowledgements: We thank the Odisha Forest Department for providing the necessary permission (Letter no: 10451/4WL-630/2018) and logistic support during the fieldwork. We also thank the director, dean, and research co-ordinator of the Wildlife Institute of India for providing us with facilities and infrastructure. We greatly acknowledge Mr. Bidya Sagar, Mr. Diganta Sovan, Mr. Pradeep Dey, Mr. Samresh Biswal, and Mr. Susanta Jena for providing their valuable assistance in the field. A special thanks to Mr. Saifuddin Mallik and Mr. Anil Fartyal for their invaluable assistance in preparing the map. Mr. Buddham Naik, Mr. Laxman Dalei, and the frontline staff of Similipal Tiger Reserve and Kuldiha Wildlife Sanctuary are acknowledged for their assistance in the field.



भारतीय वन्यजीव संस्थान
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INTRODUCTION

The Tiger *Panthera tigris* is an endangered large carnivore (Goodrich et al. 2022) that exemplifies conservation efforts worldwide. India has achieved a rare conservation achievement by implementing a strong 50-year conservation program (MoEF&CC 2023). The tiger numbers got more than doubled from a population estimate of 1411 (1165–1675) in 2006 to 3682 (3439–3925) in 2022 (Jhala et al. 2008; Qureshi et al. 2023). However, the future of these tiger populations depends on careful management of the remaining forested habitats, where they are expected to face challenges from rapid urbanisation, increasing human density, expanding agriculture and associated infrastructure development and economic growth (Gubbi et al. 2016). In the Indian scenario, it is even more important as majority of the extant protected areas (PAs) are fragmented and all the tiger landscapes of the country have not experienced similar levels of population recovery. For example, the Central-India and Eastern Ghat landscapes currently retains ~40% of India's wild tiger population inside largely fragmented wildlife habitats (Jhala et al. 2020). This landscape has experienced substantial increase in tiger abundance from 2014 to 2022, except in the east-central states of Odisha, Chhattisgarh, and Jharkhand (Jhala et al. 2021; Qureshi et al. 2023). The small, isolated tiger populations of this landscape currently face various ecological, demographic, and genetic challenges (Seidensticker 2016).

The tiger population in Odisha, in particular, is of specific conservation interest as they represent a genetically unique lineage of melanistic form in the wild (Singh 1999; Kolipakam et al. 2019; Sagar et al. 2021). Similipal Tiger Reserve (STR- 2750 km² area) in Odisha currently reports the only known breeding population of the melanistic wild tigers globally (Rathore et al. 2021) and has been identified as one of the 42 source populations of tigers in Asia (Walston et al. 2010). Historically, tigers were found across STR along with surrounding PA's of Kuldiha Wildlife Sanctuary (KWS- 272.75 km² area), Hadagarh Wildlife Sanctuary (HWS- 191.40 km² area) and in Satkosia Tiger Reserve (SkTR- 963 km² area). However, the tigers have gone locally extinct from KWS (the last Tiger died in 2009- Panda 2019), HWS (the last Tiger died in 2014), and SkTR (Qureshi et al. 2023). An intensive camera-trap based study conducted over a duration of eight months in 2013 failed to report tiger presence in KWS (Debata & Swain 2018), making STR as the only hope for this unique population as well

as in the east-central landscape.

Such recent events of local extinctions and declining tiger occupancy (between 2006–2022) (Qureshi et al. 2023) demands appropriate long-term conservation strategies through landscape-level approaches to ensure future tiger survival. The expansion of tiger occupancy along with ensured connectivity between the remnant habitats is critical for their future persistence in this landscape. Here, we present empirical evidence of a tiger dispersal from STR to KWS and discuss potential measures to be undertaken for increasing tiger occupancy in Greater Similipal (Similipal-Hadagarh-Kuldiha) Landscape.

MATERIAL AND METHODS

Study Area

The study was conducted across STR and KWS, located within the Deccan Peninsula Biogeographic Zone (Rodgers & Panwar 1988). Both areas feature tropical moist deciduous, tropical dry deciduous, and tropical semi-evergreen forest types (Champion & Seth 1968). The major large carnivores include Tigers, Leopards *Panthera pardus*, Indian Wolves *Canis lupus*, Asiatic Wild Dogs *Cuon alpinus*, Sloth Bears *Melursus ursinus*, and Striped Hyenas *Hyaena hyaena*. The ungulate prey community consists of Chital *Axis axis*, Sambar *Rusa unicolor*, Gaur *Bos gaurus*, Northern Red Muntjac *Muntiacus vaginalis*, Indian Chevrotain *Moschiola indica*, Four-horned Antelope *Tetracerus quadricornis*, and Wild Boar *Sus scrofa*. The Asiatic Elephant *Elephas maximus* is also present in both protected areas (Nayak 2014; Panda 2019).

STR and KWS are connected by two corridors along the northern and southern parts of the Salandi reservoir (Nayak 2014; Menon et al. 2017; Figure 1). The Similipal-Kuldiha corridor traverses the northern part of the Salandi reservoir along HWS and connects to a thin strip of reserve forest (ranging 0.3–2 km in width). This region is part of a proposed elephant corridor and contains six densely populated villages (Nayak 2014; Menon et al. 2017) and 97 temporarily defunct stone quarries. The forest has experienced encroachment pressures from nearby villages, posing a significant conservation challenge (Menon et al. 2017; Panda 2019)

Camera Trapping

As part of an ongoing tiger assessment program, 1,526 motion sensor camera-trap stations were placed and systematically monitored in STR from 2019 to

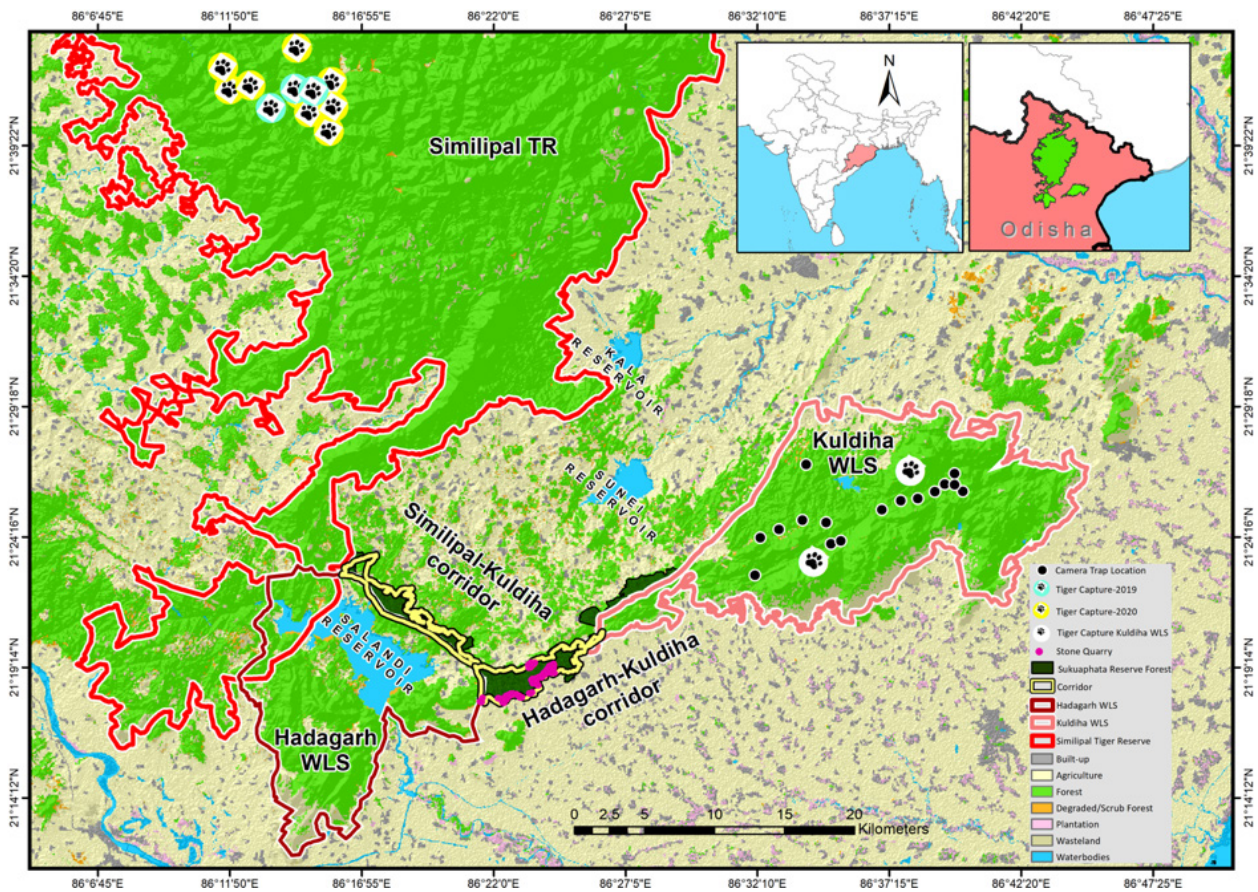


Figure 1. Map of Similipal-Hadagarh-Kuldiha protected area complex along with the biological corridors and the Tiger (T21) photo-capture locations in the years 2019, and 2020 in STR and 2021–2022 in KWS.

2022. Camera trapping was conducted in the entire core of STR following the national guideline of a 2 km² grid design to cover the intensive study area (NTCA-WII 2018). All the digitally stamped (with date and time of capture information) tiger photographs were identified and separated out from the entire data set. The individual tiger identification was performed by using the software ExtractCompare (Hiby et al. 2009). Genitalia and secondary sexual characters (such as nipples for females) were used to ascertain the gender of the individual tigers in the four-year dataset.

Initially, KWS was not part of this monitoring effort, as no tiger signs were recorded here over last decade (Panda 2019). During December 2021, local department officials reported presence of possible tiger pugmarks in KWS and immediately a monitoring exercise was planned. An intensive large carnivore sign survey was conducted across KWS based on the reports from the ground staff members. Eighteen sites (forest roads, animal trails and trail junctions etc.) were selected with high potential of tiger presence for deploying camera-

traps. Subsequently, single-sided camera traps were placed in all these sites from 22 December 2021 to 27 January 2022. The cameras were kept active throughout the day and regularly monitored. The tiger photos captured in these cameras were compared with the available tiger photograph repository from STR (Rathore et al. 2021) using ExtractCompare (Hiby et al. 2009). The results were further validated by three independent trained personnel. The age-class category assessments was conducted by using all earlier camera-trap records of the individual following Sadhu et al. (2017).

RESULTS

Two tiger images were obtained from all the camera traps deployed in KWS (Image 1c,d). The images were captured on 24 December 2021 and 8 January 2022, respectively. Both images were ascertained to be from one young-adult male tiger, which later matched with a cub (named as T21, Image 1a) earlier photographed



Image 1. Images of tiger (T21): a—photo-captured as a cub in 2019 | b—juvenile in 2020 in STR | c—Right flank | d—and left flank of T21 photo-captured in KWS in 2021–2022.

in UBK range of STR in 2019. T21 was photographed till September 2020 in the same range (Image 1b) before finally photo-captured in KWS in 2021. This dispersal event confirmed tiger presence in KWS after 11 years and indicates the possibility of an active corridor between these two PAs, where STR can be considered as the source and KWS as a sink habitat.

DISCUSSION

The STR tiger population has experienced a recent population increase from 12 ± 1 individuals in 2018 (Jhala et al. 2020) to 20 ± 2.47 individuals in 2022 (Qureshi et al. 2023). We feel that the recent tiger dispersal is possibly driven by the displacement of young individuals from STR to KWS as a result of the increase in tiger numbers. It is important to point out that although the growth of human habitation and mining activities in this space has ecologically separated Kuldiha from Similipal, but tiger movement link exists through Hadgarh WS.

Our results provide empirical evidence of tiger dispersal to this protected area, which was earlier suggested by Singh (2021). If such a rise is continued then more such events can be anticipated across the Greater Similipal Landscape, and therefore appropriate steps towards managing this region need to be planned.

PAs connected through corridors in a metapopulation framework are currently the foundation for contemporary tiger conservation initiatives (Seidensticker 2016). Considering the evolutionary importance of the STR Tiger population, their demographic and genetic challenges, and isolated habitats, maintaining the integrity of the larger Similipal-Hadagarh-Kuldiha complex will be extremely critical. Firstly, urgent management attention is warranted toward habitat restoration of both the Similipal-Kuldiha and Hadagarh-Kuldiha corridors. One of the most effective ways to achieve this would be to include HWS, KWS, and the reserve forests (RF) in this corridor within a potential revised STR boundary, where the added areas could become part of the extended buffer area of STR, where a synchronized management

plan can be implemented. Further, adequate attention towards prey recovery throughout the entire region is required, where habitat management efforts aimed at increasing large ungulate densities would be beneficial for potential tiger recovery as the relative abundance of prey species is very low in KWS (Debata & Swain 2018) and HWS (Palei et al. 2021). The prey density estimation exercises should be conducted regularly in KWS and HWS to track ungulate biomass availability. Illegal hunting/poaching of ungulate prey has been reported in KWS (Panda 2019) and thus intensive monitoring of their population and protection measures will be crucial for tiger recovery. In this regard, implementation of regular anti-poaching patrolling using MSTriPES (Monitoring System of Tigers- Intensive Protection and Ecological Status; <https://www.project-tiger.in/>) would be essential. Similarly, government-supported incentivized voluntary human settlement relocation programs will improve the habitat productivity for ungulates and would play a vital role in successful tiger repopulation in KWS and HWS. Further, attention and necessary planning towards addressing potential human-tiger negative interactions is also needed. There are 12 villages within KWS with a human population of 17,000 and a large population of livestock (Panda 2019). Considering the fragmented nature of this area and such high human presence surrounding the PAs, increasing human-tiger interactions can be expected in the near future. Tigers are known to traverse through agricultural landscapes (Habib et al. 2021), often leading to such conflict situations. For conflict mitigation, active management efforts like timely compensation plans, participatory management efforts, etc., need to be in place to reduce any chances of retaliatory tiger deaths.

It is important to point out that our data is suggestive of this active corridor between STR and KWS, as no direct evidence was available to prove tiger use of these corridors. We suggest regular monitoring and assessment programs through intensive field surveys and camera-trapping approaches to assess the prey diversity, density, habitat use, and movement patterns across KWS, HWS, and the corridor regions.

The tiger populations in the east-central region of the central-India and Eastern Ghat landscape are facing adverse impacts from various human interventions across their habitats. The STR tigers are showing encouraging dispersal signatures with surrounding habitats. We believe that the dispersal event presented in this paper should be used to prepare an appropriate and focused management plan aiming at maintaining the source-sink population dynamics thereby assisting

in long-term persistence of this evolutionary unique tiger lineage in Kuldiha and Hadgarh sanctuaries.

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ISSN 0974-7907 (Online) | ISSN 0974-7893 (Print)

June 2024 | Vol. 16 | No. 6 | Pages: 25283–25494

Date of Publication: 26 June 2024 (Online & Print)

DOI: 10.11609/jott.2024.16.6.25283-25494

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